SCANDINAVIAN TRINUCLEIDAE

WITH SPECIAL REFERENCES TO NORWEGIAN SPECIES AND VARIETIES

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WITH 14 PLATES AND 47 FIGURES IN THE TEXT

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INTRODUCTION

Prof. Dr. J. Kiær once advised me to make a study of the Norwegian Trinucleidae. He kindly allowed me to use his valuable collections of Ordovician Trinucleidae from the Oslo field.

The Norwegian forms of these trilobites have not been described since Angelin (1851—54) made a brief description in his well-known work "Paleontologica Scandinavica". The Norwegian material is found in a very good state of preservation. The fossils are usually preserved in limestone, which gives a good illustration of the morphological and structural characters. The chief part of the Trinucleidae previously described, has been preserved in more or less pressed shales which disturbs the original shapes of the fossils.

Nearly all the material examined belongs to the Paleontological Museum of Oslo. The oldest collections were made by Sars and Boeck a hundred years ago. Brøgger made a detailed stratigraphical study of the Ordovician layers of the Oslo valley. In his geological map of the islands of the Oslo Fjord (1887) he gave an excellent basis for later investigations and collections. A considerable material of Trinucleidae was collected by Brøgger from the different zones. A very large and valuable amount has been collected during later years by Kiær. Especially his collections from Ringerike have provided very interesting facts concerning the Trinucleidae. Considerable collections have also been made by Holtedahl. The author has tried to a certain extent to complete some of the earlier collections.

After having examined the material at Oslo I went to Denmark and Sweden to compare the other Scandinavian collections with our own. In Copenhagen Dr. Ravn kindly showed me the specimens of *Tretaspis* from Bornholm. In Lund the collections of Tørnquist, amongst others, were of great interest. Prof. Grønwall kindly allowed me to take some specimens from Dalarne to Oslo for examination.

In Stockholm and Uppsala I am indebted to Dr. Hägg, Dr. Warburg and Dr. Westergård who showed me the various collections. Some good specimens of Norwegian Trinucleids collected by G. Holm, as well as some specimens from Dalarne, were borrowed for description.

The methods of working out the material have been different. The small specimens have been prepared with the finest needles available.

Ignition and cooling in water have been used on the hard limestone. About 90 thin sections have been made. Dyeing has not proved useful. Many of the sections have been orientated. Serial sections have been made (about 70) of *Tretaspis kiæri*, with measured distance between each grinding. The grinding has been made by hand, and in some cases only the time of grinding has been noticed as a rough measurement of the thickness. The polished surface has been photographed imbedded in Canadian Balsam.

During the whole time of my study of the Trinucleidae, Professor J. Kiær has shown my work the greatest interest, and I wish to tender him my heartiest thanks for his valuable support, and also for the good advice he has given me. I am also indebted to Professor Holtedahl and Curator Heintz for their kind assistance during my work.

The photos have been made by Miss Lily Monsen and the author. Where the photos have been retouched, this has been done by Miss Barstad and Miss Thorbjørnsen.

HISTORICAL REVIEW

The literature concerning the Trinucleidae is very copious. BARRANDE (1852 p. 609) gives a view of the same up to 1850. *Trinucleus* occurs already in the first work on Trilobites by LHWYD 1698. In the years from 1820—1850 a number of papers were written about *Trinucleus*. WAHLENBERG (1821) described the first Trinucleid from Sweden. He was followed by DALMAN (1826) and HISINGER (1837). In Norway BOECK (1827, 1838 P. 143) mentions 4 species of Trinucleids. He only used the names of the species which were: *granulatus* WAHL., *ornatus* or *tesselatus*. STERNB., *trinucleum*, SARS et BOECK and *bronni*, SARS et BOECK. *T. bronni* was a new species. The description is very brief. The species has only two rows of pits on the fringe. This indicates *Trin. coscinorinus* described by ANGELIN (1851—54). ANGELIN does not mention the description of BOECK. LOVÉN (1845) gave very good detailed descriptions and illustrations of *Tretaspis seticornis* and *T. granulata*. He paid attention to the resemblance between *Trinucleus* and *Harpes*.

GREEN (1833) collected the known Trinucleids in the genus *Cryptolithus*. MURCHISON (1839) took up the name *Trinucleus* used by LHWYD. The generic name *Trinucleus* has since been used by European authors, but in America the name *Cryptolithus* has partly been maintained. The name used by LHWYD was established before systematic nomenclature was employed in science. Now both generic names are used for different genera of the family Trinucleidae. MURCHISON (1839. P. 659) mentioned the generic name *Tretaspis* (perforated and deeply sculptured shell). This name was later used as a generic name for one part of the Trinucleidae. ROUALT (1826) and BEYRICH (1846) gave the first detailed explanation of the double, perforated structure of the fringe, slightly indicated by MURCHISON. SALTER (1847) tried to explain the nature of the perforated fringe as a transition stage between the "non-perforated brim of *Harpes* to the spines in *Araneus*".

BARRANDE (1852) gave careful descriptions of several Bohemian Trinucleidae. The development of *Cryptolithus* during the Meraspid stages was described. The family was discussed.

ANGELIN (1851—1854) described and depicted several new species of *Trinucleus* in his beautiful, systematic work on the Scandinavian trilobites.

The later works on Trinucleidae mostly consist of systematic descriptions in connection with stratigraphy. In Sweden Trinucleids have been described by Linnarsson (1869), Andersson (1893), Olin (1906), Hadding (1913), Funkquist (1919). In Norway Kjerulf (1865), Brøgger (1887) and Holtedahl (1907) give stratigraphical contributions to the Norwegian Trinucleidae. Ravn (1899) studied the Trinucleidae of Bornholm. Raymond (1913) tried to divide the original genus *Cryptolithus* = *Trinucleus* into 3 genera: *Cryptolithus*, *Trinucleus* and *Tretaspis*. This division will be mainly followed in this work. Larger systematic descriptions of Trinucleids were made by Portlock (1843), Salter (1853, 1866), Nicholson and Etheridge (1878—80), and Reed (1903, 1914, etc.).

The zoological position of the Trinucleidae was discussed by Beecher (1895) and Raymond (1920). Beecher (1895) also gave valuable facts concerning the larval stages. Several studies have been made on the morphology of the family. Oehlert (1895) made one of the best detailed investigations of the structure of *Trinucleus*. His explanation of the closed pits cannot, however, be maintained.

The chief work on the Trinucleidae was carried out by Reed (1912—16). In his Notes on *Trinucleus* he described the different organs of the British Trinucleids. The interesting fringe is ascertained. The upper and lower lamella are described in available species. He gives a new explanation of the glabellar lobes compared with other trilobites.

Richter (1921 b) in his work on *Harpes* draws an interesting conclusion on the homology with Trinucleidae. The structure of the pits and marginal suture is ascertained. He regards the eye of *Harpes* as homologous to the usual lateral eyes found in Trilobites. This is one of the chief reasons why he does not maintain the order Hypoparia. He observes the close relationship of *Harpes Dionide* and *Trinucleus* (broad sense). Swinnerton, (1915, 1919) excludes the order Hypoparia and puts up the opistoparian *Orometopus* as an ancestor of the Trinucleidae. The last question has been opposed by Raymond and (1917) and Stetson (1927). Stetson gives an account of all known Trinucleidae and tries to work out the relationship. Warburg (1925) has also discussed the position of the Hypoparia. The results obtained by the above mentioned authors will be discussed in the general part below.

Bancroft (1929) has described several forms of upper Ordovician *Cryptolithus* from Shropshire, England. In the description of the new genera and species almost no account is given on the affinities to previously described genera and species.

SYSTEMATIC PART

The Basis of systematic Description.

The systematic classification of the family Trinucleidae has always been difficult to carry out. This is especially owing to: (1) the mode of preservation, (2) changes during growth, (3) great variation within the single species or variety.

1. The mode of preservation varies to a great extent. The Trinucleids are preserved in shales, limestones and in some cases in sandstones. In the typical Trinucleid-shales the specimens have been strongly pressed. The often bulbous glabella is broken and shows no elevation. The surface of the specimen is often beautifully preserved. The structure of the two lamellae of the fringe is in most cases easy to determine. The limestone specimens show a quite different illustration of the species. The original shape is maintained. The strongly elevated cephalon is preserved in a quite different way to that in the pressed shales. (This may be compared in Pl. II, Fig. 1 and Pl. 8, Fig. 5). The surface of the test of the specimens is often highly reticulated. The shell is therefore almost always broken off and the smooth internal cast is found. The internal cast of the fringe often gives a different image to that of the outer surface found in the slate specimens. According to this the fringe might show 4 different surfaces in the preservation: the two surfaces of each of the fringe lamellæ. Little attention has been paid to the difference between the inner and outer surfaces of each lamella.

2. Great changes during growth are not common among the genera. Usually the adult characteristics are acquired at very early stages of growth. An important exception to this is found in *Reedolithus carinatus*. This form shows a surprising change in general appearance during the late stages of growth.

3. The great variation within a single species or variety causes the greatest difficulties in systematic classification.

In the family Trinucleidae several features of systematic value are found. The different characters may develop within different genera. It is difficult to decide which component should be chosen as a basis of classification. Probably the glabellar structure gives the best index to a possible phyllogenetic connection. A glabella with the same morphological characters seems however to be able to develop independently in the two genera

Trinucleus (T. bronni and *T. bucculentus)* and *Tretaspis*. The shape of the glabella is not very well suited for systematic description, on account of the poor preservation of the number of specimens occuring in shales. Usually the structure of the fringe has also been used as a systematic component. Stetson (1927) and Bancroft (1929) especially pay great attention to the structure of the fringe. The fringe is often well preserved, and gives in the arrangement of pits good features for a distinct description. As seen below, the minute structure of the fringe is, in my opinion, to a great extent due to the main shape of the fringe. The minute structure

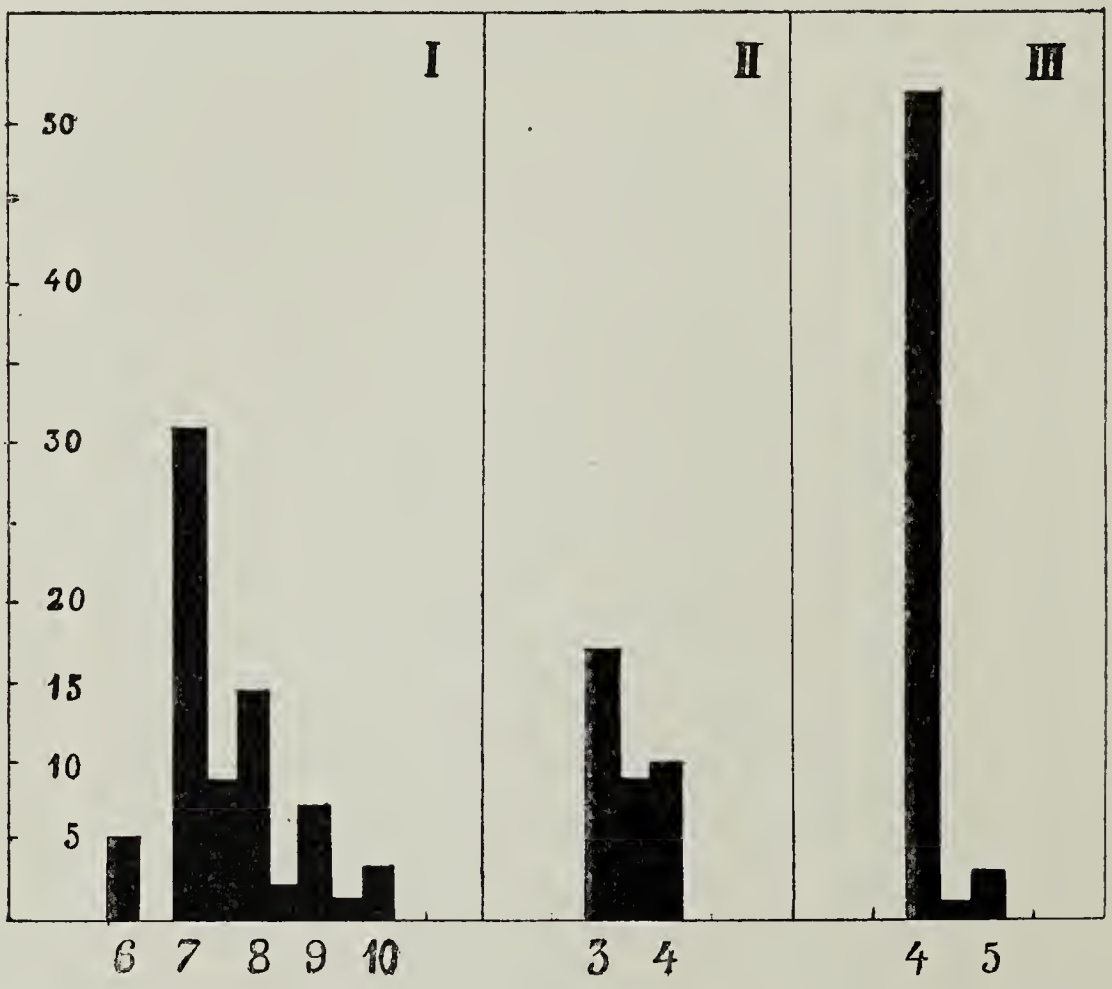


Fig. 1. Variation in the number of pits on the fringe of *Tretaspis seticornis* (His.) from Dalarne. Explanation of the graphs on 10.

only serves to strengthen the fringe, and thus is of smaller systematic value. Through convergence different genera might develop a similar structure of fringe. This is found in a number of adult specimens of *Reedolithus carinatus* which resemble the genus *Tretaspis*. Within a well-defined genus a study of the number and arrangement of pits on the fringe gives several interesting facts concerning the variation within the species and varieties. The genus *Tretaspis*, which is well represented in Scandinavian formations, has been used for statistical research. The number of pits is noticed in three different places of the fringe: I at the posterior margin, along the prolongation of the occipital segment, II across the fringe, anterior to the median line, III across the fringe anterior to the dorsal furrow. If the number of pits is visible on both the right and left side of the cephalon the average value is used. A little individual variation, assymetric arrangement and different number of pits on the right and left side of the median line is often present. A row of intercalating pits is reckoned as a half

pit. Samples of the indices might be seen in the figures of the plates: Pl. 9, Fig. 3 shows II 5 and III 5., Pl. 10, Fig. 3 a has I 12. Pl. 11, Fig. 1 shows I 7 II 3 III 4. (The outer double row is hidden in nearly round pits that indicate only one row.)

The intercalating rows of pits are usually less common than the whole rows. On III a new row is often only indicated by one to three pits. The result of the examination is shown in graphs as seen in Fig. 1.

The absciss represents the number of pits, the ordinate the number of specimens of each group of a similar number of pits. The small columns with half pits are easily separable from those with a whole number which are larger. To obtain a more even curve it has been convenient to divide the columns of half pits on each of the columns of whole pits on the sides. If the number of half pits is uneven the specimen left passes on to the column on the right which has the greater number of pits. The other Figs, 21, 32—34 shows graphs where the half pits — columns have been transferred to the whole ones.

The statistical method, much applied in Zoology, is also used in Palæontology. The investigations of Richter (1916) on *Calceola sandalina* may be mentioned.

The variation within a certain species or variety in population is illustrated by the well known Galton curve. A well marked two-topped curve indicates a mixture of two different forms. This was the basis of Richter's separation of the two forms of *Calceola sandalina*.

The morphologically much related species *Tretaspis cerioides* and *T. kiæri* have been separated on account of the curves. The species could not have been separated without this examination. The individuals of *T. cerioides* with the highest number of pits are close to those of *T. kiæri* with the fewest pits. The graphs of *Tretaspis* give a good illustration of the variation within a certain population in a certain layer and locality. The number of specimens examined is too small to make a detailed study of the character of the graphs. A mathematical discussion is not carried out. The breadth of the curves gives an idea of the width of variation. The size of variation is not very different. In some cases the variation is unusually great. This may be noticed partly in Fig. 21 a, b, of *T. cerioides* and better in Fig. 32 of *T. granulata*. In this case the two graphs a and b indicate a mixture of two forms in the curve c. This is also confirmed by the morphological studies (see p. 70). The possible mixture of forms in *T. cerioides* and *T. cerioides* var. *angelini* has not been observed.

The statistical method is very useful for the comparison of similar forms in different localities or from different layers. Two closing curves from different localities give a valuable indication of identity. The graphs of *T. seticornis*. Fig. 1, Fig. 33 b, c, Fig. 34 b—c show a small difference. The curves of the Norwegian and Ølandian forms agree, but

the Dalarne and Østergøtland specimens show some difference. In II and III the late localities show fewer pits. The same facts can be studied in *T. latilimbus*. The youngest Norwegian form (Fig. 33 g) differs especially in II from the Swedish (Fig. 34 d).

A stratigraphical variation has also been traced. Fig. 33 indicates a successive increase in the number of pits through the geological period of *T. seticornis* and *T. latilimbus* from Norway.

The statistical method gives a basis of possible determination of phyllogeny.

The statistical research of the genus *Tretaspis* clearly shows the difficulties of a natural classification of the species and varieties. No attitude can be taken as to the problem of genotypes and phänotypes. The systematic classification must be regarded as a preliminary division of the present material. My hope was by statistical research to trace a possible evolution by mutations within the different geological layers. The material has been too meagre for a solution of this interesting problem.

Terminology of morphological Description.

In the description of Harpeidae and Trinucleidae some special terms are used. In the following paper the nomenclature mainly follows Bather (1910), Reed (1914—1916) and Warburg (1925 p. 214). The smooth, semicircular fields lateral to the posterior part of glabella are called alæ. Their lateral boundaries are called alar furrows. The usual name cheek-lobes is used instead of genal areas employed by Reed. The perforated duplicated portion of the cephalon is called fringe. It is parted by the marginal suture in an upper and lower lamella. The upper lamella is often divided into a brim, (outer band) and a cheek roll (inner band). The outer raised margin of the two laminæ is called the upper and lower rim. The vertical band between the two rims will be termed the marginal band. The lower lamella is divided by the girder into an outer and inner band. The sharply edged concentric ridges on the upper lamella are called concentric lists. The dark lines in the shell within the concentric, reticulate list (on glabella) and terrace lines (on fringe) are termed stay-lines.

The earlier ontogenetic stages are termed Meraspid stages, as suggested by Raw (1925). Raw and Stubblefield (1916) has maintained the term "Degree" used by Barrande for the different Meraspid stages. In this work the more convenient term stage, abbreviated st. has been used. (see p. 59) only average dimensions are given in the systematic descriptions. A table containing the different dimensions of several specimens has not been used. The strongly arched Trinucleidae very often give wrong measures on account of pressure.

Description of Genera.

In his work on "Classification of Trilobites" SWINNERTON (1915 p. 543) places the three families Trinucleidae, Raphiophoridae and Harpedidae together in a sub-order Trinucleidae. The close relationship of this genera has also been mentioned by RICHTER (1921 b p. 214). BARRANDE (1878 p. 47 Pl. 5, Fig. 15—20) describes an interesting species which he calls *Trinucleus reussi.* RAYMOND (1917, p. 204) proposes the new name: *Trinucleoides* for the species on account of the primitive stage of the fringe. STETSON (1927 p. 98) writes: "It does not seem to me that this species belongs to the family at all". His objections are mainly the lack of radial arrangement of the two rows of pits on the fringe, and the well defined lobes of the glabella which are of the same shape and in the same position as in *Dionide*. The first objection must be ommitted since the Meraspid stage I of *Tretaspis seticornis* just shows this arrangement of pits. The lateral lobes of glabella might be compared with those found in the family Trinucleidae. STETSON does not mention the hypostoma which differs from *Tretaspis* and *Cryptolithus* and resembles *Dionide*, f. inst. *D. formosa.* BARRANDE (1852 Pl. 42. Fig. 26—27). Unfortunately the hypostomae of the trinucleidae are very rare. They can not for the present be used as definite systematic characters. The general appearance of *Trinucleoides reussi* (BARR), especially the thorax and pygidium, shows a great resemblance to the Trinucleidae. It is difficult to decide if the form has to be placed among the Trinucleidae or the Dionididae. The form certainly represents a special genus, and I suggest maintaining the name *Trinucleoides* as proposed by RAYMOND, and put the genus among the Trinucleidae.

SWINNERTON (1915 p. 543) placed the three families, Trinucleidae, Raphiophoridae and Harpedidae together in a sub-order Trinucleida. The close relationship of this family has also been mentioned by RICHTER (1921 b, p. 214). The genus *Dionide* is usually placed in the family Trinucleidae.

RAYMOND (1920, 1925, p. 21) proposes a new family Dionideidae, and thus separates the genus *Dionide* from the family Trinucleidae. WARBURG (1915, p. 70) mentions the similarities of the *Dionide* and the genera of Trinucleidae. She finds it most justifiable to include all in the same family. In the following the classification of RAYMOND is used, although the two families are much allied, and connected by the genus *Trinucleoides.*

In the family Trinucleidae RAYMOND (1925, p. 19) includes the 4 genera *Trinucleoides* RAYMOND, *Tretaspis* McCOY, *Trinucleus* MURCHISON and *Cryptolithus* GREEN.

The genus *Botrioides* proposed by STETSON (1927, p. 97), for the Scandinavian species of Trinucleus must be ommitted since the present work shows their typical Trinucleus character.

BANCROFT (1929) proposes 4 new genera within the Trinucleidae. His genus *Reedolithus* is based on the species described by REED (1903) as

Trinucleus subradiatus. The species has been referred to *Tretaspis* (Stetson 1927) and *Cryptolithus* (Ulrich 1930). The genus *Reedolithus* is maintained in this paper. The genus and the species belonging to it are discussed below.

The three genera *Marrolithus, Salterolithus* and *Reuscholithus* are characterized by the number and arrangement of pits on the fringe, and shape of the outline of the cephalon. The investigations of the present writer on the variation of pits and shape of fringe in Scandinavian Trinuclidae shows that smaller differences in those features are not very reliable as generic characters. In the genus *Salterolithus* Bancroft (1929 p. 28) mentions as a generic character, three rows of pits external to the girder. Reed (1912, p. 388) mentions, however, in his well known paper on *Trinucleus* only two rows of pits in the form used by Bancroft as a genotype. Bancroft gives no discussion concerning which of the earlier described species have to be included in his four proposed genera.

The diagnosis of Raymond of the genera of Trinucleidae are very brief, below some details are added.

Distinguishing generic Characters.

Family *Trinucleidae* Emmrich.

Genus *Trinucleus*, Murch.

Trinucleus fimbriatus Murch. genotyp.

1) Glabella with 3 distinct pairs of lateral furrows, pseudofrontal lobe more or less prominent. Upper lamella of fringe concave, with pits in radial sulci. Lower lamella with distinct girder and probably without radial sulci. No occipital spine. Lateral eye tubercles occur in some species and are reduced or lack in others. Lateral outline of thorax little arched. Posterior pleural bands strong. Arenig. — Caradoc.

Genus *Reedolithus*, Bancroft.

Reedolithus subradiatus, (Reed.) genotyp.

Glabella keel-shaped with 3 pairs of faint furrows. No prominent pseudo-frontal lobe. Fringe more or less flat tapering at variable angle, usually about 60°. Brim and cheek-roll often separated in adult specimens. Pits usually larger on the brim than on the cheek-roll. Pits concentric and partly radially arranged. Girder not very well-marked. Cheek-roll on lower lamella without radial sulci. Occipital spine present. Lateral eye-tubercles present. Lateral outline of thorax well arched, broad pleural furrows.

Pygidium small with partly triangular outline.

Llandeilo. — Caradoc.

Genus *Cryptolithus* Green.

Cryptolithus tesselatus Green genotyp.

Glabella without, or with very small, lateral furrows. No pseudofrontal lobe. Fringe flat, tapering at an angle of about 45°, with concentric rows of pits. Girder little developed, great breadth of fringe lateral to occipital furrow. Radial arrangement of pits may occur in front. No radial sulci on the lower lamella. Occipital spine present. Lateral eye tubercles absent in adult stage. Lateral outline of thorax well arched. Broad pleural furrows. Pygidium large with triangular outline and a number of rather well-marked pleuræ. Arenig? — Ashgillian.

Genus *Tretaspis* Mc'coy.

Tretaspis seticornis. (His.) genotyp.

Glabella with 3 pairs of glabellar furrows. The two posterior ones very distinct. Well developed pseudofrontal lobe. Upper lamella of fringe divided in a concave brim and slightly convex cheek-roll. The cheek-roll slants down at an angle of about 80°. Carrying more or less radially arranged pits. The brim carries pits in radial sulci. The lower lamella with distinct girder and radial sulci on the cheek-roll. No occipital spine. Lateral eye tubercles usually present.

Lateral outline of thorax slightly arched.

Caradoc?, Ashgillian.

Genus *Trinucleoides* Raymond.

Trinucleoides reussi (Barr.) genotyp.

Glabella with 3 pairs of faint glabellar furrows and pronounced lateral lobes. Vertical spine on the top of the glabella. Fringe with 2—3 rows of concentrically arranged small pits. Lower lamella unknown. Occipital spine and lateral eye-tubercle absent.

Lateral outline of thorax slightly arched.

Pygidium with triangular outline.

Arenig.

Stetson (1927) has grouped all known species in the genera: *Trinucleus, Cryptolithus* and *Tretaspis*. Unfortunately very few of the species have been described in detail. The lower lamella of the fringe is very often unknown. The following species seem to belong to the genus *Reedolithus*: *R. carinatus* Ang. (1854), *R. reticulatus* Ruedm. (1901), *R. richthofeni* Kayser (1883), *R.? radiatus* Murch. (1839) is little known, but probably belongs to this species. The arenig *Trinucleus sedgwichi* Salter (1866) and *T. gibbsi* Salter (1866) show great resemblance to this genus. They are too little known to provide a decision.

I almost agree with the grouping of the different species by Stetson. The *Trinucleus Krügeri* Hoek seems to me not to be a *Cryptolithus*, but a *Trinucleus* of the *foveolatus-bronni* group.

Description of Species.

Genus *Trinucleus* Murch (p. 14).

Trinucleus foveolatus. Ang.

Pl. I, Fig. 4—13.

Trinucleus foveolatus Angelin 1851—54, p. 85, Pl. 41, Fig. 2.
Trinucleus efflorescens. Hadding. 1913, p. 75, Pl. 7, Fig. 21.
— *coscinorrhinus* — — p. 74, Pl. 7, Fig. 20.

Distinguishing characters. "Glabella with slightly prominent" pseudofrontal lobe. Cheek lobes very broad and flat. Fringe of even breadth all round the cephalon. Upper lamella with deep radial sulci holding about 4—6 rows of small pits. Lower lamella with girder within the first row of pits. The 3—5 rows on the inner band do not lie in radial sulci. Pygidium with narrow rachis".

The drawings and short descriptions made by Angelin give little information of the species. Unfortunately none of the original specimens of Angelin's Trinucleidae are left. I have made a neotype (ar. 2310) which in all main features corresponds to the drawing of Angelin.

General description.

Cephalon broad, semi elliptic, usually two-fifths as long as it is wide. Glabella distinctly limited anteriorly where a shallow furrow separates the fringe. The dorsal furrows gently arched backwards. The anterior part shows a very distinct antennuary pit. Glabella strongly arched. No distinct pseudo-frontal lobe. Surface smooth at the steep anterior and lateral part, but reticulated with round or long meshes on the top. Usually the reticulation consists of more or less concentric lines round a distinct, small median tubercle (Pl. 1, Fig. 13). The tubercle is most prominent on internal casts which indicate a thin shell above the tubercle. A distinct ridge is visible from the med. tubercle backwards to the occipital furrow. It gives the glabella a carinate appearance. Two lists from the median tubercle anterio-laterally are faintly indicated.

3 pairs of glabellar furrows visible. 1st pair small, situated just anterior to the issue of the ocular ridges. 2nd pair distinct, short, elliptic, transversely situated. 3rd pair goes from the axial furrow anterio-medially. Occipital furrow shallow without lateral pits.

Cheek lobes of great breadth. Surface very flat medially, but tapers steeply against the fringe. The bending line nearly forms a straight line from the antennuary pit to the genal angle. The two bands divided by the line show distinct differences. The outer band is smooth while the inner band is distinctly reticulated. Reed (1916, p. 118 and 171) gives a careful discussion of this line of which he says: "may possibly be regarded

as marking the line of fusion between the free and fixed cheeks". In my opinion the line only indicates the bending of the surface. The smooth outer band might be compared with the similar steep sides of glabella. The ocular ridges with the lateral eye-tubercles are more or less distinct. In some cases they are nearly quite absent. They disappear easily in a poor preservation. Pl. 1, Figs 4, 10 show the rudimentary character. The occipital segment is bounded anteriorly by a narrow occ. furrow. No occ. spine is found on the occ. ring. The fringe has about the same width all

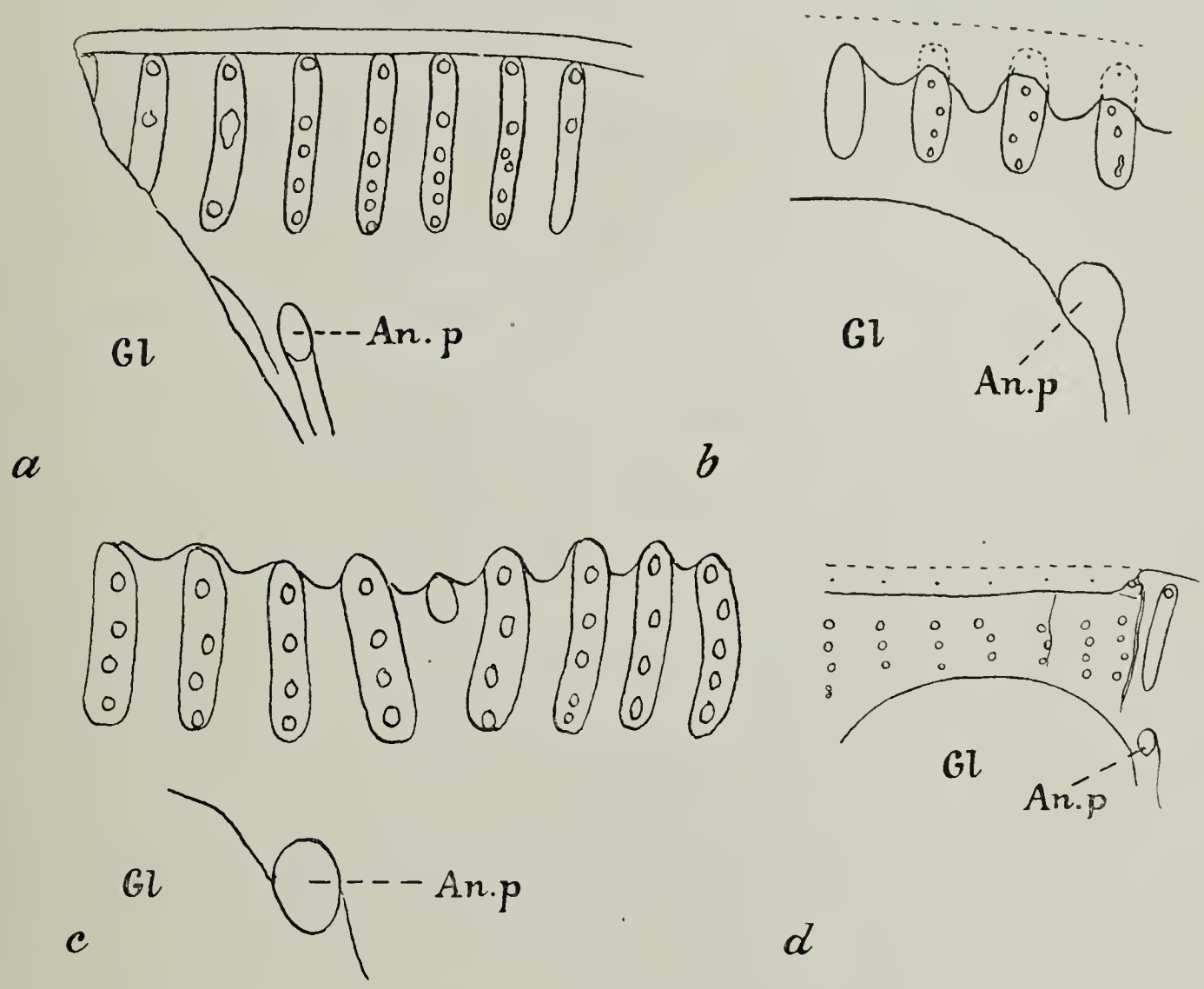


Fig. 2. Arrangements of pits on the fringe of *Trinucleus foveolatus*, Ang. *a*—*c* (H 392, Ar 2315, H 536) found in the Ogygia shale near Oslo, *d* in Jämtland. *a*, *c* belongs to Pal. Mus. Oslo, *b* to Riksmus. Stockholm, *d* to Sveriges Geol. unders. *a*—*c* × 26, *d* about × 15. *gl* = glabella. An.p. = antennuary pit.

round the cephalon. The post-lateral angles are not prolonged backwards.

The upper lamella concave, tapering at an angle of about 45°, with about 40 deep radial sulci. It has been very difficult to trace the pits at the bottom of the sulci. In some cases the pits have been prepared. Fig. 2 and Pl. 1, Fig. 12 show the pits in sulci. The pits lie more or less radially arranged in the sulci. The number is 4—6, which seems to vary greatly.

The upper rim narrow. Marginal suture on the upper part of the marginal band. Lower lamella of fringe only observed in a few specimens. Fig. 2 d shows the structure consisting of a narrow outer band with one

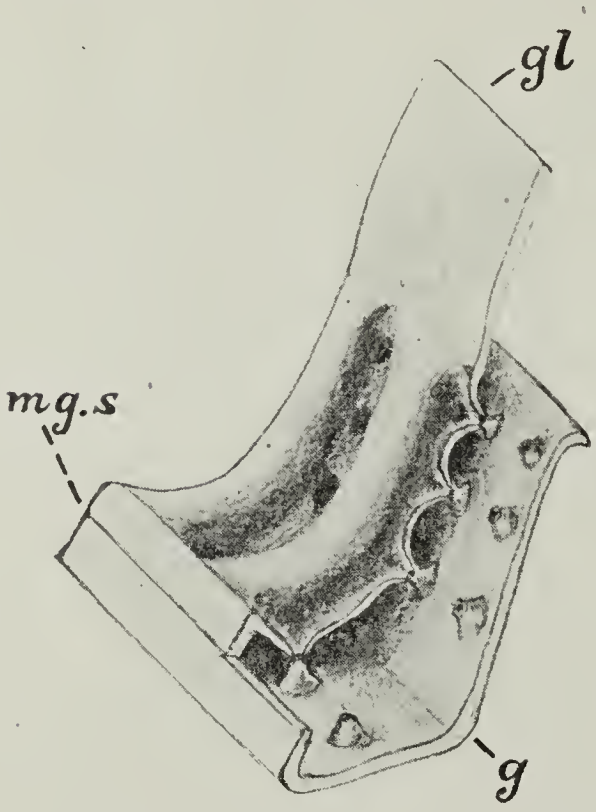


Fig. 3. Restored portion of anterior fringe in *Trinucleus foveolatus* Ang. Both lamellae visible. *Gl.* = glabella. *mg.s* = marginal suture. *G* = girder.

row of pits, a distinct girder and a flat inner band. Pits small, indicating very short hollow pillars. The specimen described as *T. efflorescens* by Hadding (1913) which I have had an opportunity of examining, shows the lower lamella with 3—4 rows of pits. The girder angle ca. 120°, one row of pits on the outer band. Genal spine is shown on the figure of Hadding (Fig. 3). A restoration of the fringe is given on Fig. 3.

Thorax unknown.

Pygidium broad with narrow rachis.

The most typical specimens are seen on Pl. 1, Fig. 7, 8. Rachis with about 7 segments. They agree with the drawings of Angelin. The pygidium depicted by Hadding shows great resemblance and probably belongs to this species and not to an *Ampyx* as Funkquist suggests (1919 p. 35). Pl. 1, Fig. 9, 11 shows two pygidiae found together with cephalons of this species. The poor state of preservation admits no distinct determination, but they are more like *T. bromi* than the typical specimens of this species. On Pl. 1, Fig. 9 a larval stage with keeled glabella and prominent lateral eye-tubercles is depicted.

Dimensions. Average length of cephalon 3,5 mm, breadth 9—10 mm; of pygidium 2 mm and 7 mm.

Affinities are discussed p. 28.

Occurrence. The species is found in the lower and middle Ogygia shale near Oslo, and in the Mjøsen district. In Sweden it occurs in Jämtland and Scania.

Trinucleus foveolatus Ang. var. *intermedius* n. var.

Pl. 1, Fig. 1—3.

One beautifully preserved specimen (H 391) differs in some characters from the usual type of *T. foveolatus*. The two forms seem to approach each other. The systematical divisions are only preliminary as long as a sufficient material is not present.

General description.

Cephalon of semielliptic outline. Glabella well arched, with faint median tubercle and a median list posterior. 3 distinct pairs of glabellar furrows.

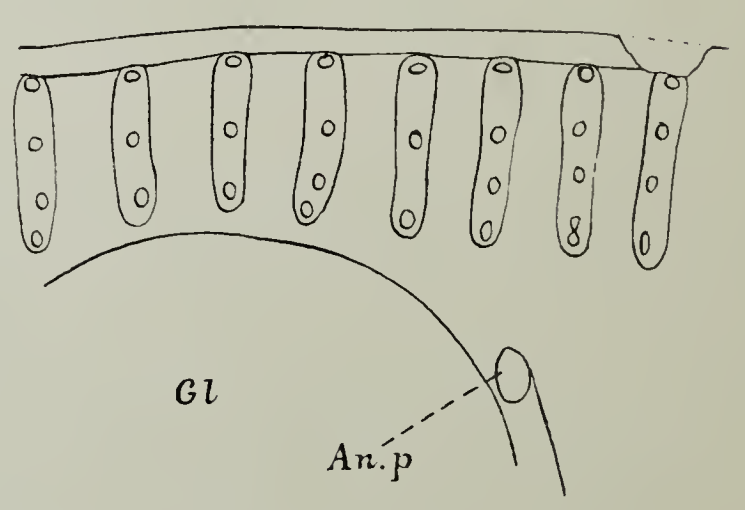


Fig. 4. Arrangement of pits on the fringe of *Trinucleus foveolatus* Ang. var. *intermedius* n. var. 20. Ogygia shale Asker. Compare Pl. 1 fig. 1.

Antennuary pits. Gently arched cheek lobes without a distinct bending line. Lateral eye tubercles well marked.

Fringe with 40 deep radial sulci. No posterio-lateral prolongation. The number of pits is seen in Fig. 4. The number of pits-rows is 3—4. A fifth row is indicated.

Ventral fringe, thorax and pygidium unknown.

Dimensions. Length of cephalon 4 mm, breadth 8,5 mm.

Affinities. This variety shows a close resemblance to *T. foveolatus*, differs in the smaller breadth of cephalon, the little developed bending line of the cheek lobes, the prominent lateral eye-tubercles, and the few pits in the radial sulci.

Occurrence: Ogygia shales Asker by Oslo.

Trinucleus bronni (Sars et Boeck).

Pl. 2. Fig. 1—7.

Trilobites Bronni Sars et Boeck 1838 p. 143.
Trinucleus coscinorinus Angelin. 1851—54 p. 65, Pl. 34, Fig. 4.
—„— Hadding 1913 p. 74, Pl. 7, Fig. 18. 19.
—„— Funkquist 1919 p. 34, Pl. 1, Fig. 7—22.

Distinguishing characters. "Glabella broad, reticulated, with prominent pseudofrontal lobe. Arched cheek lobes with eye tubercles. Upper lamella of fringe with 2—4 rows of pits in deep radial sulci. Lower lamella with one row of pits outside a distinct girder. Pygidium short with broad rachis".

Boeck 1838 mentions a new *Trinucleus* from Norway which is characterised by two rows of pits on the fringe. He probably meant this species. On examining the collections in the Pal. Museum of Oslo I found some specimens of this species determined by Boeck as *T. bronni*. One of these specimens (cotypes) has been chosen as a lectotype. *T. bronni* is not mentioned by Angelin who gave the first illustration of this species. The description of Boeck is very brief, but since specimens determined by him exist, I have maintained his name for the species.

General description. Cephalon semielliptic to semicircular in outline. Glabella bulbous. Semispheric pseudofrontal lobe. Surface reticulate with fine meshes. Internal cast smooth or with fine granulae. Median eye-tubercle scarcely visible on the surface, but distinct on the internal cast. 3 pairs of glabellar furrows of which the first pair is nearly obsolete. 2nd pair short, distinct, nearly transversely situated bounding the pseudofrontal lobe. 3rd pair runs anterio-medially from the axial furrow at the lateral portion of occ. furrow. Axial furrows broad with antennuary pits in front. Axial furrows usually appear very deep on account of pressure.

Cheek lobe arched, surface reticulated with small round meshes. Lateral eye tubercle present but not well developed. The smooth internal cast shows traces of the eye ridge.

The fringe has not been closely studied in the earlier works on this species. The authors mentioned only give one row of pits on the fringe. The Norwegian material has shown the structure of the fringe. The fringe is narrow, upper lamella with about 32 short radial sulci of which the two posterior are usually reduced. A faint prolongation backwards of posterio-lateral portion. The sulci holds 2—3 pits in front and 3—4 posteriorly. (Pl. 2, Fig. 3). The upper rim narrow. Broad marginal band with the suture visible dorsally. Lower lamella with a distinct girder (Pl. 2, Fig. 2, 5, 6, 7). Girder angle about 90°. On Pl. 13, Fig. 8 and Fig. 42 the girder is scarcely visible. The section is probably taken obliquely posterior. The figure gives a good idea of the hollow pillars and

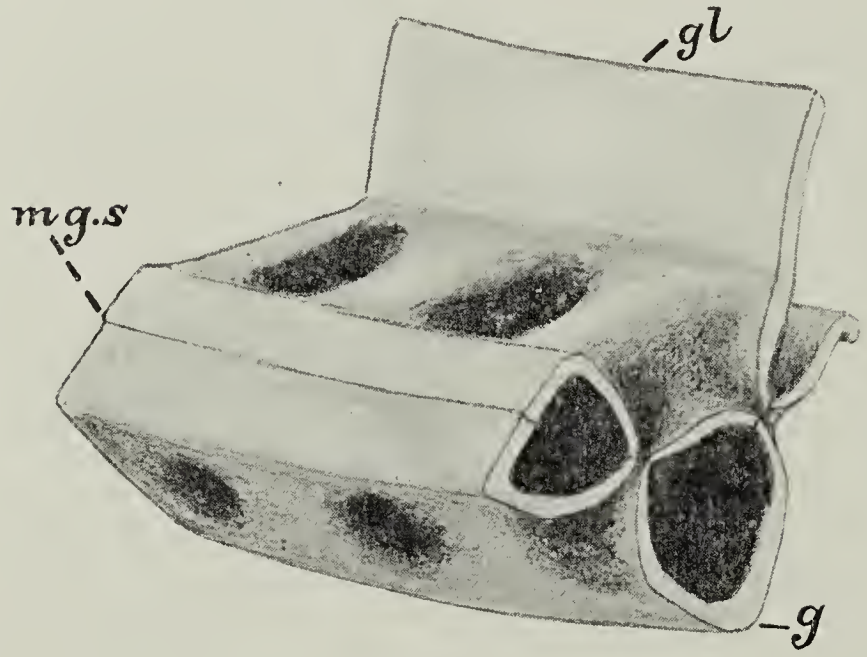


Fig. 5.

Fig. 5. Restored portion of anterior fringe. *Gl.* = glabella, *mg.s* = marginal suture. *G* = girder.

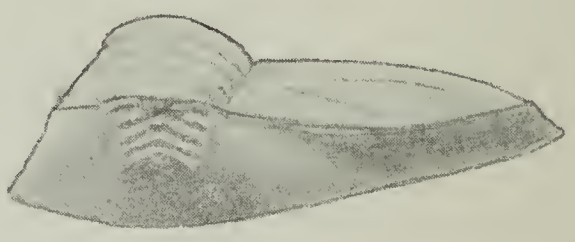


Fig. 6. *Trinucleus bronni* (Sars et Boeck). × 10. Pygidium from Tomarp Scania. Posterior view showing appendifers (specimen figured by Funkquist 1919. Pl. 1, Fig. 14).

the marginal suture. The outer band carries one row of pits. Medially the pits are largest and an indication of radial sulci may be traced. The inner band is flat or concave (Pl. 2, Fig. 7), narrowing in front. It carries 1—2 rows of pits without radial sulci. The pits on upper and lower lamella always correspond. A restoration of the fringe is given in Fig. 5. Genal spines exceed the length of body.

Thorax rectangular in outline. Rachis broad. Posterior pleural band strong. The lateral part of pleura bent backwards in all 6 segments of thorax.

Pygidium. The Norwegian specimens fully agree with those described by Funkquist. Rachis broad, cut transversely by the broad posterior band. Only few segments visible on the rachis. The pleurae are indicated by raised ridges comparable to the posterior pleural band on thorax. I have had an opportunity of examining the material of Funkquist. His Pl. 1, Fig. 14 shows a finely preserved internal cast. Fig. 6 gives a drawing of this specimen to show muscular impressions on the posterior band. At least 5 pairs of appendifers are indicated. (See p. 93).

Dimensions: Average length of cephalon 4 mm, breadth 9 mm, (without genal spines), median length of body 9 mm. Length of pygidium 1,5 mm, breadth 6 mm.

Affinities are discussed p. 28.

Occurrence. The species is rare in the typical Ogygia shale, but occurs abundantly in the upper sandy part of the Ogygia shales where it indicates a determined zone. Specimens are found near Oslo, at Eker and Ringerike. In Sweden in Scania.

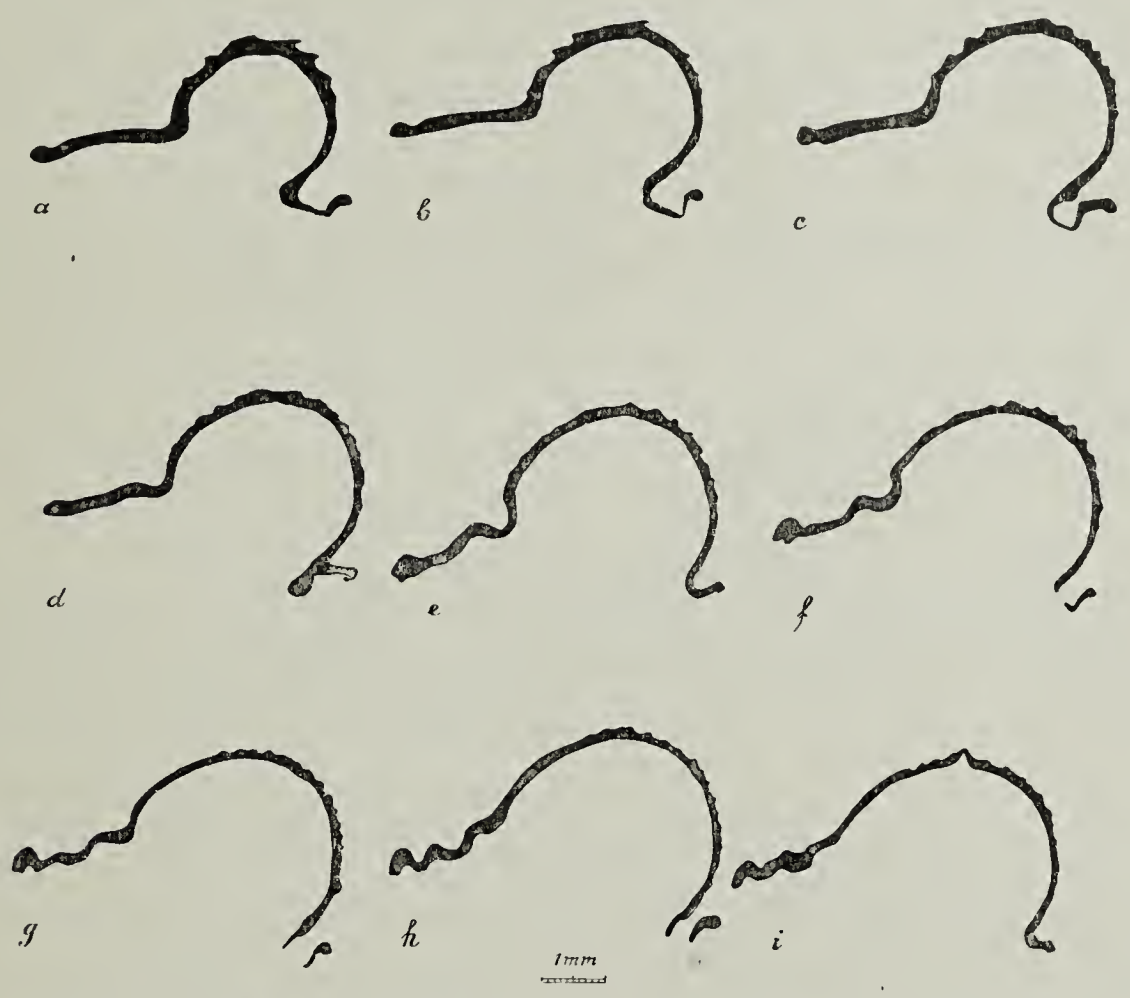


Fig. 7. *Trinucleus bucculentus* ANG. × 5. Ogygia shales, Asker. (Kiær coll. belongs to Pal. Mus. Oslo). Longitudinal sections of glabella and upper lamella of fringe. *i* shows median tubercle. Distance between each polished surface nearly the same. (30 sek. grinding).

Trinucleus bucculentus ANG.

Pl. 2, Fig. 8—15.

Trinucleus bucculentus ANGELIN 1851—54 p. 84, Pl. 41, Fig. 1.

Distinguishing characters. "Very prominent glabella. The bulbous anterior part quite overhanging the anterior fringe. Glabella with concentric lists. Arched cheek lobes. Fringe very narrow in front. Upper lamella with 1—3 pits in radial sulci. Lower lamella with 2—3 pits. Distinct girder within the 1—2 outer rows of pits which anteriorly lie in faint radial sulci. Pleuræ on pygidium well marked".

Only a very few specimens exist of this interesting species which has been considered to be the most primitive of the known Trinucleidae. The present material has been prepared and serial sections and two thin sec-

tions have been made. This quite illustrates the morphological structure. ANGELIN's original is lost, and H 480 is taken as a neotype of the species.

General description.

Cephalon with semicircular to semiparabolic outline. Glabella large, strongly arched, shows great resemblance to the genus *Tretaspis*. Pseudofrontal lobe very well developed, semi-spheric. 1rst pair of glabellar furrows very faint, 2nd pair distinct, 3rd pair oblique, partly communicating with the deep lateral pits of the shallow occipital furrow. Glabella shows a very marked reticulation. The surface is provided with concentric narrow ridges or lists, to a great extent resembling the terrace lines common among trilobites. A little median eye tubercle is found on the surface of the shale. The internal cast shows a prominent med. eye tubercle, indicating a thin shell above the eye. Pl. 13, Fig. 4 illustrates the cross section of the eye. Fig. 7 gives an idea of the thick test. The internal cast is provided with fine impressions (Pl. 2, Fig. 13) indicating fine granulæ on the lower surface of the shell. The granulæ are not found beneath the glabellar furrows, where the shell is smooth. On the internal cast a median ridge is found backwards from the med. tubercle. A pair of oblique lists are also indicated in several specimens. The lists end in 2 or 3 pits. This is shown in Fig. 8. Similar shapes are found in *Tretaspis*. The ridges on the upper surface of the specimen are indicated on the lower by fewer granulæ.

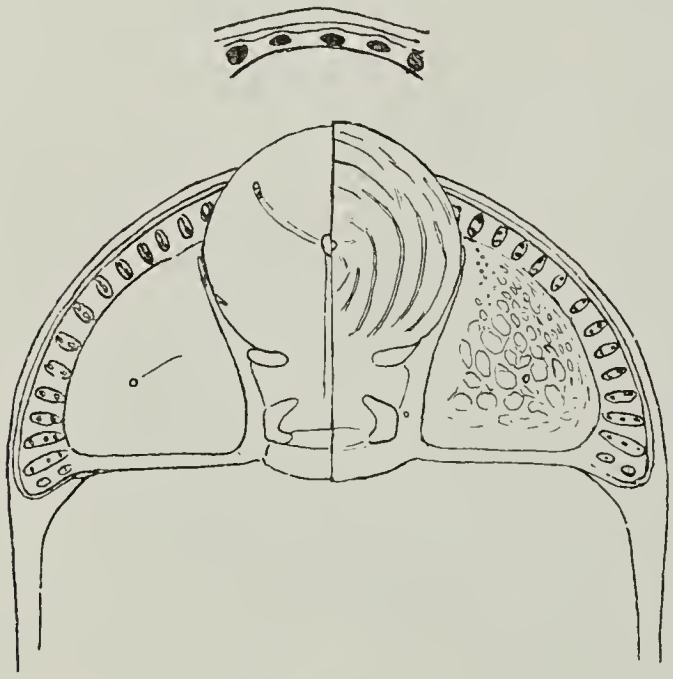


Fig. 8. *Trinucleus bucculentus* ANG. Restored cephalon. Inner cast on the left side. Above the hidden portion of fringe.

Axial furrows narrow anteriorly, ending in the deep antennuary pits. Posterior part of axial furrow is broad and shallow. Cheek lobes arched, surface reticulated. Anteriorly near fringe the reticulated surface is followed by small elevated points. The lateral eye tubercle is only known in the inner casts. It is very small, smaller than the median eye tubercle.

The fringe is very narrow seen dorsally. Anteriorly the narrow fringe is hidden by the bulbous glabella (Fig. 8). The fringe drawn by ANGELIN shows a narrow fringe of the same breadth round the cephalon, bearing one row of pits. The present material shows an upper lamella very narrow anteriorly, but a little broader posteriorly. In front there is only one row of very short pits visible. Laterally the pits become radial sulci with 2—3 pits. The number of pits near the margin is about 32.

The marginal band is visible dorsally carrying a distinct marginal suture in the upper part. The lower lamella has been prepared in some

specimens. Pl. 2, Fig. 16 shows the lower surface of the lower lamella. Pl. 2, Fig. 9 and 12 indicates the lower lamella below the upper. To obtain a true illustration of the structure of the fringe serial sections have been used.

The intervals between each polished surface have not been measured, but the time of the grinding (by hand) is the same = 10 seconds.

The cross sections of the fringe are taken near the axial furrow anterior to the cheek lobe. The sulci have been hit obliquely. The marginal suture line is not visible on the polished surfaces.

Fig. 10 shows a thin section taken in the median line in front of glabella. It gives a good impression of the small portion of the fringe visible dorsally.

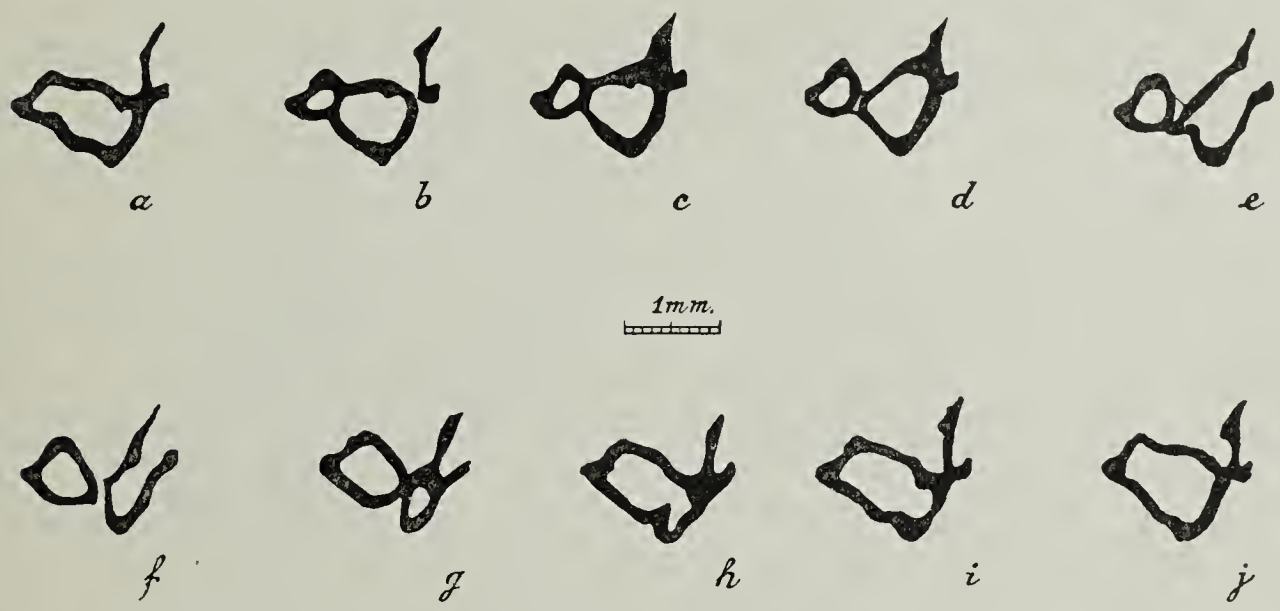


Fig. 9. *Trinucleus bucculentus* Ang. × 7,5. Ogygia shale, Asker. (Kiær coll. belongs to Pal. Mus. Oslo). Serial sections across the fringe. Nearly the same distance between each polished surface. (10 sek. grinding).

The marginal suture follows a raised line on the upper part of the marginal band. The lower part of the band concave. Lower rim with terrace lines. A distinct girder with terrace line separates the outer and the inner band. Girder angle ca. 120° anteriorly, 90° anterio-laterally.

The outer band contains one or two rows of pits anteriorly. Pits in shallow radial sulci opening forwards. Laterally only one row is found in the narrow band. Inner band has one row of pits. Posteriorly more rows arise. As seen in Fig. 10 the inner row of pits represent the openings of long hollow pillars. The two lamellæ are well separated from each other. The integument attachment lies at the basis of the fringe. Fig. 11 gives a restoration of the fringe in front of glabella.

The round pits on the upper lamella do not represent a single row of perforations of the fringe but are the common openings of three rows of pits on the lower lamella. The structure cannot be regarded as very primitive.

Thorax. A beautifully preserved enrolled specimen has been found (Pl. 2, Fig. 14, 15). The outline of the 6 segmented thorax seems to be as in *T. bronni*. Rachis well arched, rather narrow, broadest in the 3rd

segment. Articulating half ring separated from the ring by a deep articulating furrow carrying deep lateral pits (appendifers). Articulating ring with a faint short keel and indication of granulated surface. Pleuræ with distinct fulcrum. Inner part shows a narrow anterior band, separated from the posterior band by a pleural furrow, very narrow near the rachis, but widening laterally. The posterior band is provided with an unusually strong oblique ridge. Pygidium broad. Proportion 1 : 3,7. Rachis with 4 distinct segments. Pleuræ faintly granulated, indicated by elevated ridges as in thorax.

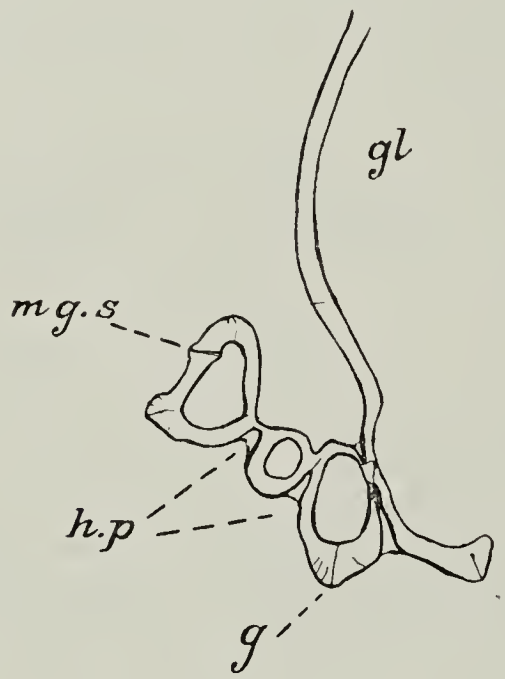


Fig. 10. *Trinucleus bucculentus* Ang. ca. 10 ×. Ogygia shale Asker (Kiær coll. belongs to Pal. Mus. Oslo) *gl.* = glabella. *mg.s* = marginal suture. *h.p* = hollow pillars. *g* = girder.

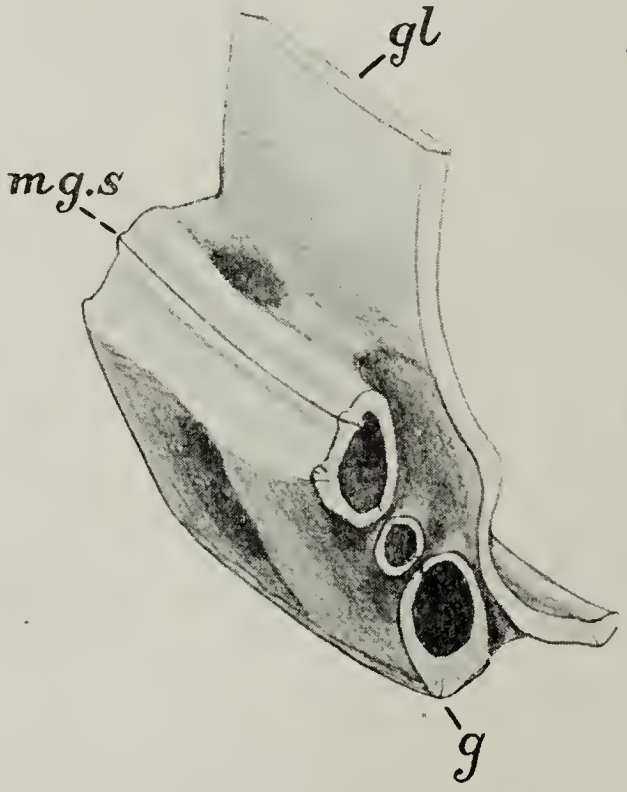


Fig. 11. *Trinucleus bucculentus* Ang. Restored portion of anterior fringe. *gl* = glabella. *mg.s* = marginal suture. *g* = girder.

Dimensions: Average length of Cephalon = 10 mm, breadth 18 mm. The length is more than double of the other *Trinucleus* species described in this paper. Length of pygidium 2,5 mm, breadth 8,5 mm.

Affinities. This species shows the greatest resemblance to *Trinucleus hibernicus* which has a similar broad anterior part of outer band of lower lamella. The affinities will be further discussed on p. 28.

Occurrence. Ogygia shale near Oslo where it is rare. Brøgger (1887 p. 17) mentions also Ampyx limestone.

Trinucleus hibernicus Reed var. *bröggeri* n. var.

Pl. 3, Fig. 1—14.

Distinguishing characters. "Glabella with pseudofrontal lobe, reticulated surface. Cheek lobe strongly arched with lateral tubercle. Fringe broadest in front. Marginal band flat. Upper lamella with shallow radial sulci carrying 2—3 rows of pits. Lower lamella with a broad outer band

having deep sulci and radial ridges in front. 1—2 rows of pits on outer band and 1 on inner band".

General description.

Cephalon semi-elliptic in outline. Glabella broad, strongly arched. Pseudo-frontal lobe most prominent in the largest specimens, but not very well marked off from the posterior part of glabella. The front of glabella partly hides the anterior fringe. 3 pairs of glabellar furrows. 1rst pair very faint, situated just in the middle of the distance between the antennuary pits and the 2nd pair of furrows. 2nd pair of glabellar furrows deep, short, oval, forming a deep impression in the anterio-medial part of glabella. Posterio-lateral part shallow. 3rd pair also deep, especially anteriorly. Running from the axial furrow anterio-medially. Laterally they communicate by a shallow furrow with the lateral pits in the occipital furrow. The shell of glabella very thick. Median tubercle present as a small smooth pustule on the upper surface of the specimen. The larger tubercle on the internal cast shows a thinning of the shell above the tubercle. Surface of shell reticulated with rather round meshes. Round the med. tubercle a concentric arrangement of the lists is indicated. Axial furrows wide and shallow posteriorly, becoming narrower and deeper anteriorly forming the antennuary pits. Anteriorly a shallow furrow goes round the base of the glabella.

Cheek lobes strongly arched, rather narrow. On the highest point the lateral eye tubercles are found. The posterior part very steep against the occipital segment.

The surface of the shell has a particular structure (Pl. 3, Fig. 11). The lat. eye tubercle consists of a smooth pustule gently elevated from the surrounding cheek lobe. The internal cast shows the thinning of the shell in the tubercle. The eye tubercle is surrounded by a ring of reticulating meshes, having the character of a "sclerotical" ring. It must explained as a structure serving to strengthen the shell. The cheek lobes have a well marked reticulation partly concentrically arranged round the lat. eye tubercle. Occipital furrow deep.

The fringe has its greatest breadth anteriorly and is more narrow posteriorly. The two lamellæ are separated by a very distinct marginal suture, situated on the broad marginal band. The band is different to that in most Trinucleidae. It is flat, tapering slightly from the inner part of the fringe down to the anterior outline. The marginal suture passes over the base of the occipital spine. Most specimens lack the lower lamella. H 553 has both lamellæ preserved and has been chosen as a holotype.

Upper lamella tapering at an angle of 45°. About 27 radial sulci in the inner part. Distance between sulci anteriorly about the double of that posteriorly. The sulci are unusually shallow. Only 2—3 rows of pits visible. Anteriorly only 2 rows are visible.

The lower lamella is highly spesialized. Pl. 3, Fig. 10 (H 563) shows the outer band seen ventrally. The band is unusually broad anteriorly. The restored detail Fig. 13, the sections Fig. 12 and Pl. 3, Fig. 8, 9 give an impression of the particular structure. Anteriorly very deep radial sulci are found extending nearly up to the upper lamella. They contain two pits. The spaces between the anterior sulci are developed as prominent radial ridges.

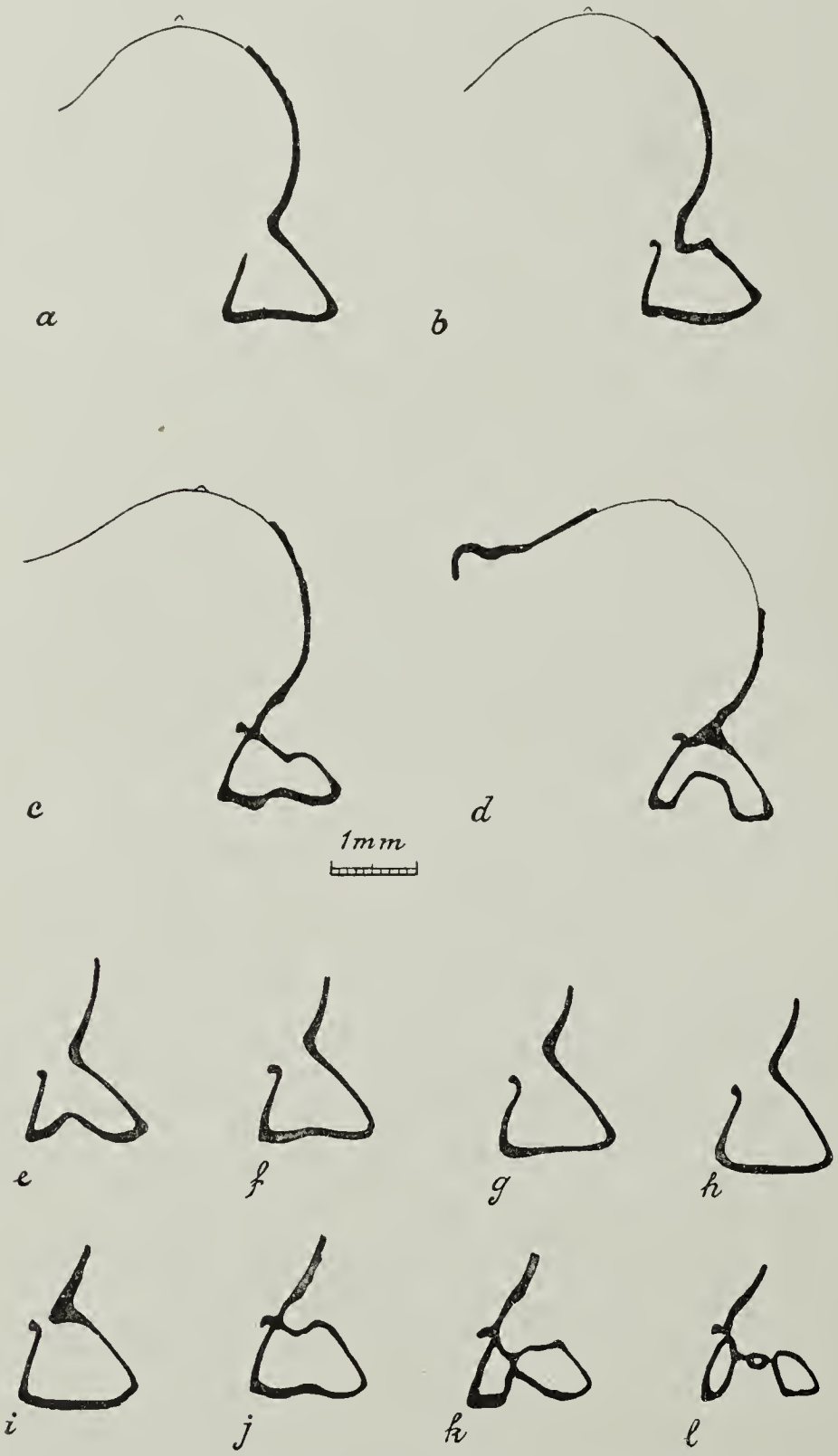


Fig. 12. *Trinucleus hibernicus* REED. var. *bröggeri* n. var. Ampyx limestone Gullerud, Ringerike. (BRØGGER coll. belongs to Pal. Mus. Oslo). × 7,5. *a*—*d* longitudinal sections of glabella with fringe. *e*—*l* sections of fringe. *a*—*d* with nearly the same distance (= 20 sek. grinding). *e*—*l* with smaller distances (10 sek.).

Girder very prominent with an angle between outer and inner band of about 80°. Terrace lines present. Laterally the deep pits are transformed into two large single pits. Outer band continues in the base of the genal spine.

The inner band has a distinct list at the top serving as an integument attachment. Just beneath the list a row of very small pits can be perceived. (Pl. 3, Fig. 8). They are indicated on the drawings of the sections Fig. 12. The pits represent the outer openings of hollow pillars communicating from the lower to the upper lamella.

Thorax not known with certainty.

Pygidium found in several specimens. A small pygidium Pl. 3, Fig. 12 measuring 0,6 mm in length and 2—4 mm breadth shows larval characters. The articulating rings on rachis continue laterally without a distinct axial furrow. The proximal part of pleuræ more elevated than the adult specimens with a semi-oval posterior outline. Rachis broad with 3—4 segments. The two anterior rings represent one segment but the posterior rings each represent

one segment. The proximal part of pleuræ not elevated as in the larval stage. 3 pleuræ visible. Rachis cut off by the broad posterior band.

Posteriorly a raised ridge which bounds the posterior band. The band is provided with terrace lines and shows 4 pairs of black spots, appendifers.

Dimensions. Average length of cephalon 3,5 mm, breadth nearly 7 mm. Length of pygidium about 1,5 mm, breadth 4,8.

Affinities. This variety closely resembles the species *Trinucleus hibernicus* described by Reed (1895, Pl. 3, Fig. 2—7) especially in the

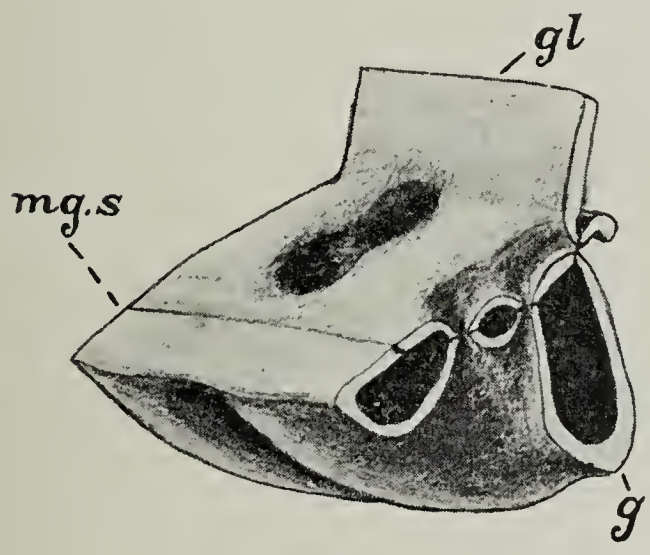


Fig. 13.

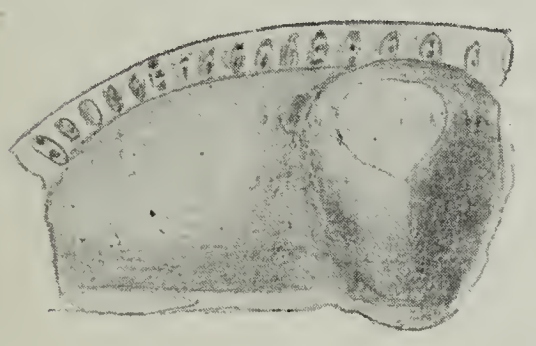


Fig. 14.

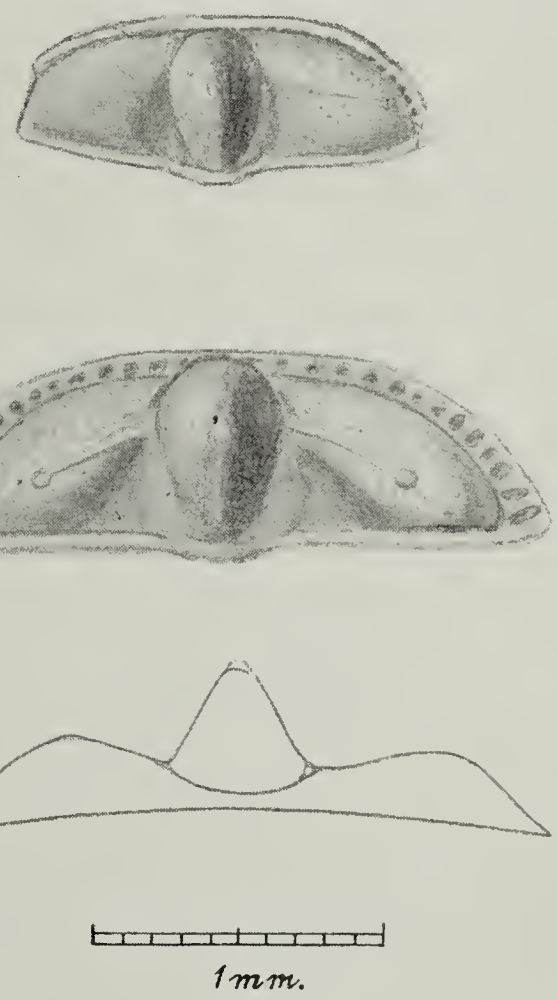


Fig. 15.

Fig. 13. *Trinucleus hibernicus* Reed. var. *bröggeri* n. var. Restored portion of anterior fringe. *gl.* = glabella, *mg.s* = marginal suture. *g* = girder.

Fig. 14. Larval stages of *Trinucleus* sp. × 23. From Ampyx limestone Gomnæs, Ringerike (auct. coll. belongs Pal. Mus. Oslo) *a* = H 410, *b*—*c* = H 414. *b*—*c* somewhat restored. Both impressions.

Fig. 15. Larval stage of *Trinucleus* sp. × 23. From Ampyx limestone Gomnæs, Ringerike. (Auct. coll. belongs to Pal. Mus. Oslo). H 415.

more specialized character of lower lamella, and the round meshed reticulation. It differs in the more elevated cheek lobes, the stronger reticulation, the stronger radial list on lower lamella. Further affinities will be discussed on p. 28.

Occurrence. Abundant in some layers of Ampyx limestone (4 $\alpha\beta$) at Gomnæs and Norderhov in Ringerike. The specimens are usually imbedded in an intraformational conglomerate.

Larval Stages of the Genus *Trinucleus*.

A cephalon of *T. foveolatus* and a pygidium of *T. hibernicus* var. *bröggeri* have already been mentioned. (Pl. 1, Fig. 9, Pl. 3, Fig. 12). At Gomnæs in Ringerike some young larval stages of *Trinucleus* were found in the Ampyx limestone. Of adult specimens *T. bronni* and *T. hibernicus* var. *bröggeri* were perceived. As those species show a near relationship it is not probable that the larval stages were very different.

The smallest specimen measured 0,55 mm in cephalon length (Fig. 14 a). Glabella carinate. The impression indicates a prominent median eye tubercle and a broad backwards pointed ridge. Cheek lobes reticulated. Lat. eye tubercle and alar fields not visible. This might be due to bad preservation. The shell seems to have been very thin. It is bent on one side. Narrow fringe present. Laterally one row of small pits visible. H 414 has a length of cephalon = 0,7 mm. Cephalon very broad. Glabella carinate (see Fig. 14 c) with traces of a larger median tubercle and ridge. The posterior glabellar furrows faintly indicated. Well developed occipital segment. A very faint ridge passing obliquely over the occipital segment at the axial furrow, continuing in alar fields. The alar furrows very broad posteriorly where they form a triangular flat space. The lateral eye with eye ridges developed. Fringe narrow but near the adult stage.

The later stages are characteristical by the broad cephalon. The carinate glabella grows broader and less elevated.

H 415 with a cephalon length of 1,05 mm (Fig. 15) is of interest on account of its great resemblance to *T. foveolatus*. *T. foveolatus* probably does not occur in those layers. The young stages of *T. bronni* or *T. hibernicus* var. *bröggeri* are very like the adult *T. foveolatus*. The fringe which suggests *T. bronni* is fully developed.

Relationship of the *Trinucleus* Species.

The present material is not sufficient for a distinct determination of the variation of the different species and varieties. As indicated above, it has been very difficult to confine the different forms. It is very probable that transition forms can be found which exclude a separation of some species. The arrangement and number of pits on the fringe are often very difficult to decide. The specimens of *T. bronni* described by Hadding (1913, Pl. 7, Fig. 18—19) are very difficult to determine. They show in the shape of the cheek lobes resemblance to *T. foveolatus*.

The following characters have been used for classification:

1) outline of cephalon, 2) shape and size of glabella, 3) elevation of cheek lobes, 4) structure of fringe. Fig. 16 gives a view of the known Norwegian *Trinucleus*.

1) *Trinucleus foveolatus* is very wide. The var. *intermedius* is a little narrower. It makes a transition to *T. bronni*, *T. bucculentus* and *T. hibernicus* are only a little narrower than *T. bronni*.

2) Glabella (Fig. 16,3) small in a—b. Bigger with pseudo-frontal lobe in c and d, and very prominent in e, which shows a strongly developed pseudo-frontal lobe.

3) Cheek lobes (Fig. 16,4) flat with a steep anterior band in a. From b—d the lobes grow more and more arched and the bending line in front vanishes. d is similar to c.

Fig. 16. Norwegian *Trinucleus* species.
a = *T. foveolatus* Ang. *b* = *T. foveolatus* Ang. var. *intermedius* n. var. *c* = *T. bronni* (Sars et Boeck). *d* = *T. hibernicus* Reed., var. *bröggeri* n. var. *T. bucculentus* Ang. 1) = Anterior portion of fringe. Lower lamella visible on the left and upper lamella to the right of the median line. 2) Cross sections of fringe anterior. 3) = Cephalon without lower lamella. 4) = Anterior view of cephalon.

4) The fringe (Fig. 16, 1,2) shows the same general shape in a—c. Specimens with 5, 4, 3, 2 rows of pits are found. d, e show different shapes of fringe. Both have two rows of pits, on outer band, lower lamella, (Specimens with only one row are, however, found in d). The particular shape of e is probably due to the great expansion of the glabella.

The facts stated above indicate a close relationship between the species. It is of interest to find a fairly parallel change in the characters of the different forms. This is especially prominent in *Trinucleus foveolatus* — *foveolatus* var. *intermedius* — *bronni*. *T. foveolatus* is the oldest

species, *T. bronni* the youngest. The ontogeny of these forms shows young stages with broad cephalon, narrow glabella without pseudo-frontal lobe, flat cheek lobes. This indicates *Trinucleus foveolatus* as the most primitive of the *bronni*-group.

Usually the species with the fewest rows has been regarded as the most primitive on account of the ontogeny of the fringe, Stetson (1927, p. 95). The phyllogeny will be further discussed below (p. 80).

Stetson (1927) records the following species of *Trinucleus:*

T. sedgwicki, T. gibbsi, T. praecedens, T. murchisoni, T. etheridgei, T. fimbriatus, T. diademata, T. acervulosus, T. foveolatus (= *T. efflorescens*), *T. bronni* (= *coscinorinus*), *T. bucculentus, T. hibernicus, T. albidus.* His new genus *Botrioides* founded on drawings of Scandinavian species cannot be maintained. I agree with him in separating an *etheridgi-murchisoni*-group.

Perhaps the little known *T. praecedens* Kloučeк (1916) belongs to this group. The arenig species *T. sedgwicki* and *T. gibbsi* must probably be put in one group. *T. diademata* Ruedm. is difficult to etablish. The fringe may perhaps represent an inner band of a lower lamella, the structure cannot be decided but possibly it is related to *T. foveolatus. T. fimbriatus* and *T. acervolosus* differ from the other species on account of the developed posterior-lateral portion on fringe.

T. foveolatus, T. bronni, T. bucculentus, T. hibernicus, T. albidus make a natural group. To this must be added the two species found in Bolivia, *T. boliviensis* Lake (1906), *T. krügeri* Hoeck (1912), *T. boliviensis* is very like *T. bronni* and *T. foveolatus,* especially younger specimens of the first. Lake (1906) mentions *T. bronni,* but states: "The glabella is not so prominent, and it is much more constricted towards the base." *T. krügeri* shows great resemblance to *T. foveolatus.* The shape of fringe of *T. krügeri* only occurs in this group. The lack of glabellar furrows caused Stetson (1927) to place the species in the genus *Cryptolithus.*

Genus *Reedolithus* Bancroft (p. 14).

Reedolithus carinatus (Ang.)

Pl. 4, Fig. 1—13. Pl. 3, Fig. 1—8.

Trinucleus carinatus Angelin 1851—54, p. 65, Pl. 34, Fig. 3,3 a.

Distinguishing characters. "Glabella strongly elevated, carinate. Glabellar furrows distinct. Occipital spine. Large lateral eye tubercle. Broad fringe with 5—6 concentric rows of pits anteriorly, up to 10 posteriorly. Partly radial arrangement of pits, radial sulci might be present on the brim. Lower lamella with girder, one row of pits on outer band, no radial sulci on inner band. Thorax Cryptolithus-shaped. Pygidium short with triangular outline."

The drawing and short description of Angelin give little idea of the characters of this species.

Examining the Norwegian material, a considerable number of specimens were found which seem to me to be identical with the species described by ANGELIN, the original of which is lost.

The material consists of about 65 good specimens and a number of fragments preserved in limestone. The preparation of the small carinate forms has been very difficult. As described below the morphological characters vary to a great extent within specimens of little size difference. A small material would very probably have led to a separation of at least two species.

A shorter description will be given of the adult stage, mainly based on the neotype H 460.

General description. Cephalon of semi-elliptic outline, with genal prolongations of fringe.

Glabella strongly arched. No pseudo-frontal lobe, but anterior part well rounded. Lateral sides of glabella rather flat. Small median eye tubercle with median ridge extending backwards against the occipital furrow. Posterior part of glabella carinate, surface of glabella reticulated anterior to the median eye tubercle. Reticulation is found anterior to the lines, corresponding to those found in *Tretaspis* of muscular function (Fig. 40, p. 96). 3 pairs of glabellar furrows of which the first pair is nearly reduced; the two posterior ones short but distinct. Lateral lobes present. Occipital furrow shallow, with marked lateral pits. Occ. ring with strong occ. spine broad at the base, rising at an angle of about 30°, length about 1 : 3 of glabella.

Axial furrows distinct with antennuary pits.

Cheek lobes well arched with a steep band against the fringe. The band is smooth, but the rather flat inner part of fringe is reticulated Pl. 5, Fig. 13). The reticulation is reduced in some specimens (Pl. 4, Fig. 12). Lateral eye tubercles unusually big (Pl. 4, Fig. 12) of elliptical outline. Not very elevated, but most laterally. The position of lateral eye is near the genal angle. This is only found in larval stages of other species of Trinucleidae. Occipital segments with occ. furrow well marked. Fringe very broad, angle of slope very variable from about 40—80°. Laterally the fringe can be very steep.

Upper lamella often concave, the brim is more or less marked (Pl. 4, Fig. 9, 10, Pl. 5, Fig. 11, 13, 17). When the brim is well marked from the cheek-roll radial sulci often are present. (Pl. 4, Fig. 3). The pits, or hollow pillars, are arranged in concentric rows. a radial symmetry is often indicated. (Pl. 5, Fig. 9, 11). The two outer rows usually a little larger than those on the cheek-roll. The outer surface of the shell shows concentric list. (Pl. 4, Fig. 11, Pl. 5, Fig. 13). The number of pit rows are 5—6 in front, laterally new rows are developed until the number is about 10 posteriorly. The arrangement of pits is shown in Fig. 17. The marginal suture runs like a raised line on the marginal band, crosses the base of genal spines and transverses the posterior margin of fringe. The lower

lamella is divided by a distinct girder. Girder angle about 120°. In some specimens concentric ridges (secondary girders) are found within the girder They are (Pl. 5, Fig. 18) like those found in *Cryptolithus*. The ventral surface of the lamella shows terrace lines. An inner list must be explained as integument attachment. The arrangement of pits agrees with that on the upper lamella. Pl. 5 Fig. 18 shows intercalating rows of pits, and a new inner row raised by division of pits. This division has been developed through radial sulci (Pl. 4, Fig. 9, Pl. 5, Fig. 18). The inner sulci on the lower lamella are also probably due to the concavity of the ventral surface.

Genal spine faintly convex, the anterior portion elevated from the base-plan of the cephalon. Section of spine nearly triangular.

Thorax. Some complete enrolled specimens occur (Pl. 5, Fig. 16, 1, 2.). In the enrolled specimens the posterior band of pygidium lies close

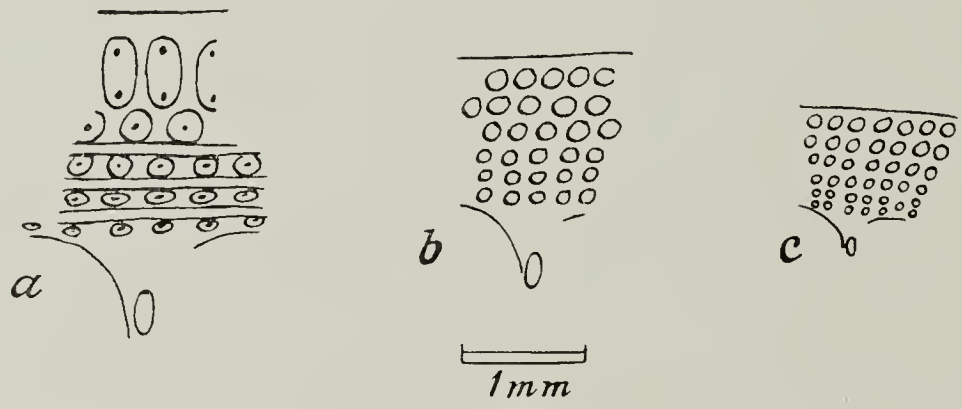


Fig. 17. *Reedolithus carinatus* (Ang.). × 10 Arrangement of pits on the fringe anterior to the antennuary pit. *a* = H467, *b* = H 435, *c* = H 441. Ampyx limestone *a* from Gullerud, *b*—*e* from Gomnæs, Ringerike. (*a* Brøgger coll. *b*—*c* Kiær coll. belong to Pal. Mus. Oslo.)

to the lists of the integument attachment on the upper part of lower lamella. In this way the inner part of body is quite closed in the enrolled position. The lateral outline of thorax convexes as in the genus *Cryptolithus*. Greatest width at the 2nd. and 3rd. of the six segments. Rachis about 2/3 of the width of the pleurae. Articulating furrow very distinct, with deep appendifers as in *Tretaspis*. Pleurae very flat. No distinct fulcrum. Pleural furrow broad and prominent. Anterior and posterior band of about the same size (different to *Trinucleus*). Laterally the pleura are bound by a vertical band, a continuation of the posterior band of pygidium.

Pygidium broad with nearly trangular outline. Length about 1/5 of breadth. Rachis of about 4 visible segments. Deep appendifers visible. Very faint pleura. Lateral part concave, bounded by a posterior ridge. Posterior band nearly vertical with terrace lines.

Dimensions. Average length of adult cephalon about 4 mm, breadth 9—10 mm. Length of body (median line) about 7,5 mm. Length of pygidium 0,8 mm, breadth 4 mm.

R. reticulatus RUEDM. (RUEDEMANN, 1901, Pl. 3, Fig. 11, 15—20) shows slightly developed lateral eye tubercles and few rows of pits on the fringe. Lower lamella is not known. It is possible that *Trinucleus diademata* (REUDEMANN, 1901. Pl. 3, Fig. 12—14) represents an inner band of lower lamella of this form. In that case it differs to a great extent from *Reedolithus carinatus* which has no radial sulci on the lower lamella.

R. subradiatus REED (1906, p. 12, Pl. 2, Fig. 1—6) has the same general characters as *R. carinatus*. Both lamellae of fringe are known. Lower lamella shows no radial sulci. The species differs from *R. carinatus* in the great number of rows of pits. *R. radiatus* MURCH. resembles *R. subradiatus*. *R. richthofeni* KAYSER (1883, p. 39, Pl. 3, Fig. 6) shows resemblance. The drawing is however not sufficient for detailed study, but the form

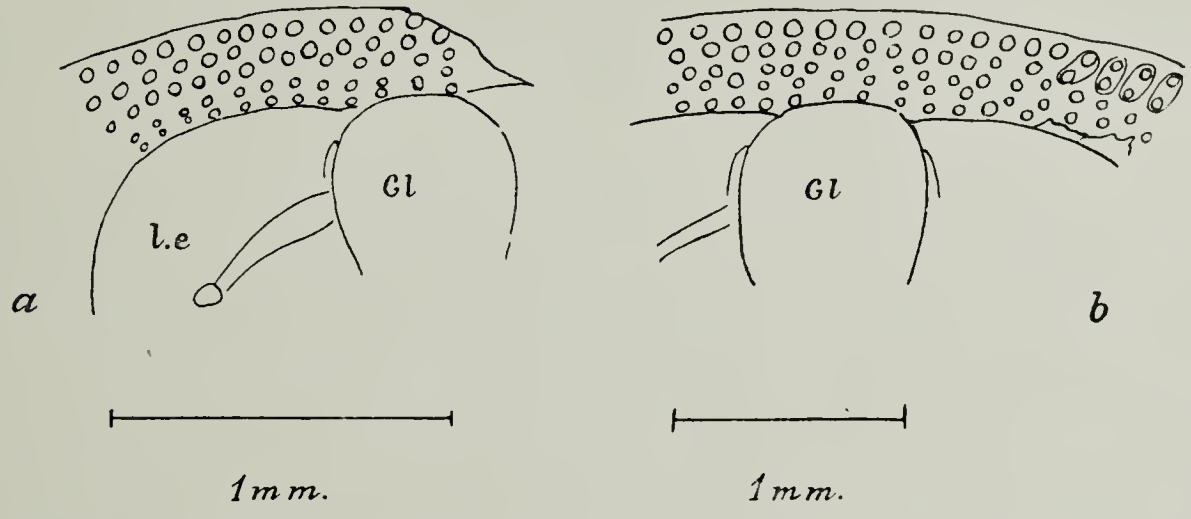


Fig. 18. *Reedolithus carinatus* (ANG.) *a* × 18, *b* × 26 Larval stages. Arrangement of pits on the fringe. a = H 518, b = H 520. Ampyx-limestone (?) Huk, Oslo. (Brøgger coll. belongs to Pal. Mus. Oslo.) Gl. = glabella, l. e. = lateral eye tubercle.

probably represents an early Trinucleidae not unlike *Reedolithus* and partly like *Trinucleus* of the *sedgwicki* group.

Occurrence. The species is found in Norway in the Ampyx limestone (4 α β). It is reported from the Ogygia shale, but it is probably not found in lower beds than the lower part of Ampyx limestone. In Norway the species is found at Huk and Asker near Oslo, on Ringerike on the localities Gomnæs and Norderhov where it is accompanied by *Trinucleus hibernicus* var. *brøggeri*, *Remopleurides* etc. It is found partly in an intraformational conglomerate. The species is known from the "Fossum Limestone" in the Skien—Langesund district. Examining the collections in Uppsala this species was found in the collections of Prof. WIMAN from Jämtland. He mentions (1897, p. 273) the species as *Trinucleus* sp. from the Chasmops limestone. According to the occurrence in Norway those layers probably correspond to the Ampyx layer, below the Chasmops layer.

The Ontogeny of *Reedolithus carinatus*. (Ang.).

This species is preserved in limestone which gives a true impression of the original shape of the trilobite. In the youngest stages of the Norwegian like the specimens of Barrande (1852) of *Cryptolithus ornatus*, it is difficult to study the finer details.

In the following the most important stages are described. No complete specimens were found of the younger stages.

The smallest cephalon (H 514) measures 0,45 mm in length. Glabella carinate, with traces of median tubercle. Glabella not divided by transverse furrows, only slightly narrowed posteriorly by two faint furrows. Distinct alae. Occipital ring little developed. Cheek lobes broad and flat. Lateral eyelists and tubercles absent probably on account of the preservation. Anterior and lateral portion of the flat cheek lobes sloping very sharply down to the narrow fringe. The upper lamella developed as a narrow, flat, smooth band, pits not recognized.

The next stage found has a length of cephalon of 0.65 mms. Carinate glabella. Lateral eye lists present, short transverse. Resembling those found by Beecher (1895, p. 307). The detailed structure cannot be determined. Fringe shows marked differences from the earlier stage. Several rows of pits are already developed.

With a cephalon length of 0,8 mm (H 420, H 531) (Pl. 4, Fig. 5—7) the later appearance is nearly attained. Cephalon broad, average length and breadth 1 : 3. Glabella carinate. Occipital ring well marked. Glabellar furrows not visible. Alae or lateral lobes faint, but well marked from the median portion of glabella.

Cheek lobes resembling the former stage. Lateral eye lists distinct, long oblique, extending from the axial furrows posterio-laterally against the genal angle. Small eye tubercles present. Fringe well developed, rather broad laterally. Genal prolongation faintly indicated. The detailed arrangement of pits on upper lamella cannot be determined. Pl. 4 Fig. 5—6 show a lower lamella of fringe. Anteriorly 4 rows of pits are separable. Girder present within the first row. Partly radial arrangement of pits. On this specimen the genal spine is preserved. No distinct genal prolongation. Genal spine is different from that of the later stages. It is usually broad showing resemblance to the posterior prolongation of the brim in *Harpes*. The phylogenetic value of this cannot be decided. It is perhaps only an adaption to pelagic mode of life.

The later growth stages will be discussed together. The morphological characters are described in the different stages up to the adult.

Glabella shows great changes in the late growth stages. Reed (1914, p. 350) discussed the nature and limits of the glabella in Trinucleidae. He found that the true course and behaviour of the axial furrows have been usually neglected in the earlier descriptions of Trinucleidae. The longitu-

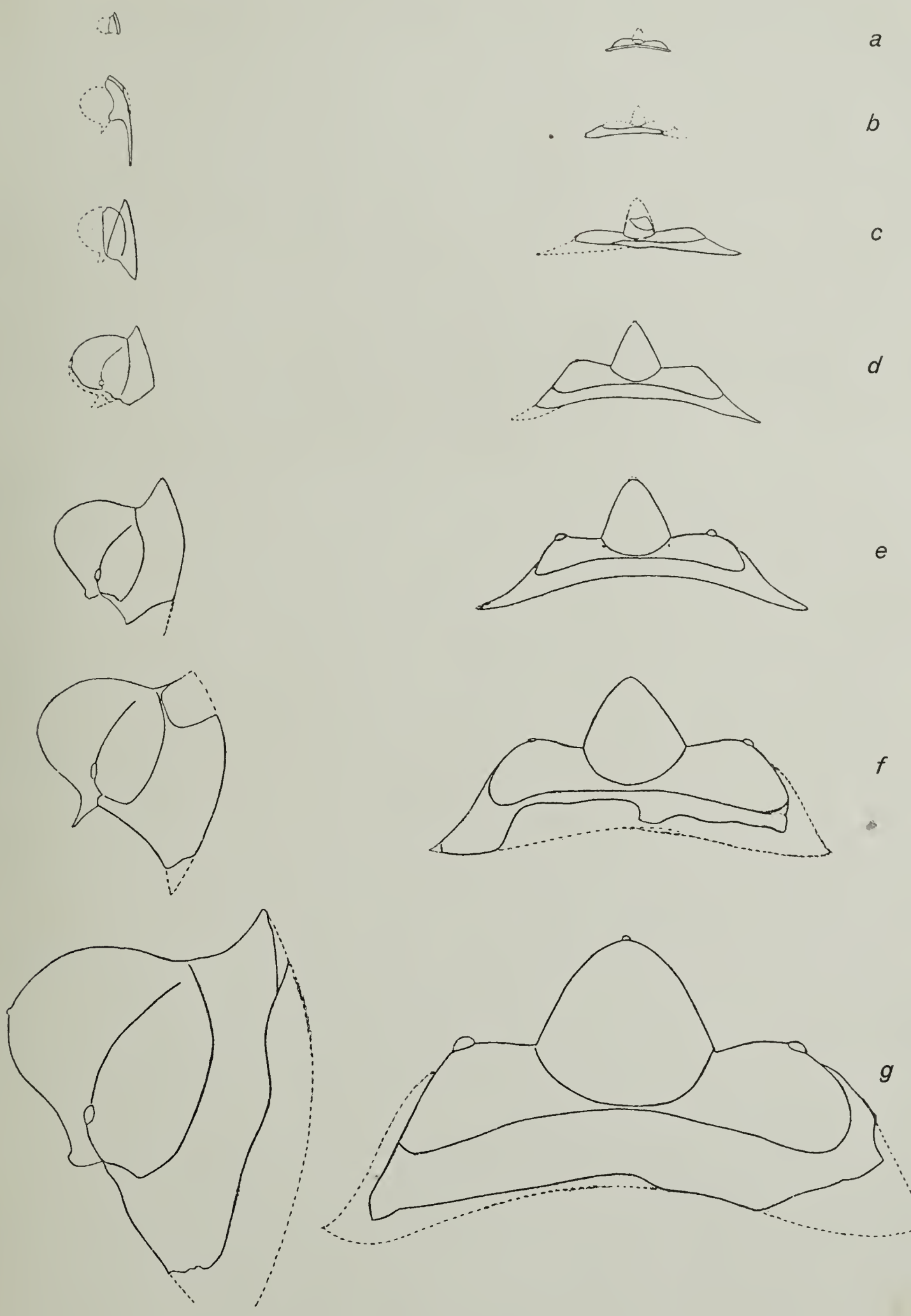


Fig. 19. *Reedolithus carinatus.* (Ang.) × 7,5. Shape of glabella and fringe during the development. Lateral and frontal view. *a*—*g* = H 514, H 531, H 518, H 520, H 441, H 515, H 460. *a*, *b*, *e*, *g* from Ampyx limestone Gomnæs, Ringerike (Kiær coll. Pal. Mus. Oslo). *c*, *d*, *f* from Ampyx limestone Huk, Oslo. (Brøgger coll. Pal. Mus. Oslo).

dinal depressions bounding the stalk on each side of the glabella e. g. in *Tretaspis* have been explained as the axial furrows.

Reed shows that these furrows are comparable with longitudinal furrows bounding a median lobe of glabella in some species of *Acidaspis* and *Lichas*. A more or less composite lateral lobe is present in Trinucleidae as in several species of *Ampyx*. Reed found this very distinct in *Trinucleus fimbriatus* (Reed, 1914, Pl. 28, Fig. 1—3) from Llandeilo. According to Reed the axial furrows go laterally to the lateral lobes of glabella in Trinucleidae. Reed has not studied the ontogeny of the lateral lobes and the course of the axial furrows.

The alae, representing the lateral lobes in the earliest stages, are well marked from the median portion of glabella. Although the alae are well separated from the median portion of glabella the ontogeny shows that they must be regarded as a part of glabella. (confr. p. 37).

The median portion of glabella is rather badly preserved in the youngest stages. Only impressions are available. The smallest specimen with glabella preserved is H 520 with a cephalon length of 1,6 mm. The posterior part of glabella however is broken off (Pl. 5, Fig. 2). Of specimens with a cephalon length of 1,8—2,5 mms, several well-preserved are present. Pl. 5, Fig. 3—8 gives an idea of the glabella.

Glabella is very strongly elevated. It has been difficult to prepare the narrow keel-shaped glabella. Usually it has broken off.

Lateral sides of glabella nearly flat, communicating at the top forming a sharp carina. In some cases a narrow list is indicated from the occipital furrow anterior to the median tubercle. The carina continues a little anterior to the median tubercle. Anterior glabella arched. During growth the flat sides of glabella become arched, the carina diminishes. This is well marked in the growth series in Fig. 19.

The median tubercle largest in the smallest stages. In the smaller specimens the surface of glabella is usually smooth (Pl. 5, Fig. 3). In the largest specimens the anterior portion of glabella is reticulated, usually in the portion anterior to the median tubercle between two diverging lines. That is the arched part of glabella.

The internal cast of glabella shows fine granulae as in the other genera of Trinucleidae. In distinct portions of the specimen the granulae are lacking. These fields are indicated as darker spots on the upper surface of the specimen (Pl. 5, Fig. 3—4). The spots are well-marked when the fossil is bedded in alcohol. The spots are very distinct in the younger specimens. The spots are drawn in Fig. 20. They are rather big. The nature and explanation of them are discussed p. 93. In the later stages the spots are sunken in the glabellar furrows. Glabellar furrows very faint in the smaller stages. In the later stages the 1rst pair of glabellar furrows appears as small oval shallow impressions down at the axial furrows. The 2nd. pair is well marked only in the latest stages. 3rd. glabellar

furrows seem to be first developed, appearing laterally and growing anterio-medially. The ontogeny of the occipital spine is not known.

The development of the lateral lobes of glabella can be studied in the present material. As described above the earliest stages have a well marked carinate glabella. An oblique furrow separates a triangular field from the cheek lobe. The alae are separated from the median part of glabella by its flat surface different to the steep lateral sides of glabella. Fig. 19 gives an illustration of the shape of the furrows lateral to glabella in four different stages of growth.

In later stages (Fig. 20 b) the triangular field (alae) becomes narrower. A division of the fields is indicated. The lateral portion is represented by a broad shallow furrow, or depressed field, making a continuation of the axial furrows anteriorly. The median portion is represented by a narrow faintly elevated portion tapering slightly laterally from the base of the median portion of glabella. The median glabella is at this stage well bounded by its steep lateral sides. At a later stage (Fig. 19 c) the broad shallow furrow laterally becomes narrower. The arched portion of the cheek-lobes grows near the posterior part of glabella. In H 516 (Pl. 5, Fig. 3 and Fig. 20 c) the median or alar field seems to be connected with the occipital ring. The occipital furrow does not pass through the elevated alar field. At this stage the alae are less marked from the central portion of glabella. The alae are more elevated and the lateral sides of glabella become a little less steep. In the adult, (Fig. 20), the furrow bounding the median part of the cheek lobes is quite longitudinal, forming a natural axial furrow according to Reed. The alae or lateral lobes (Reed) have become stee-

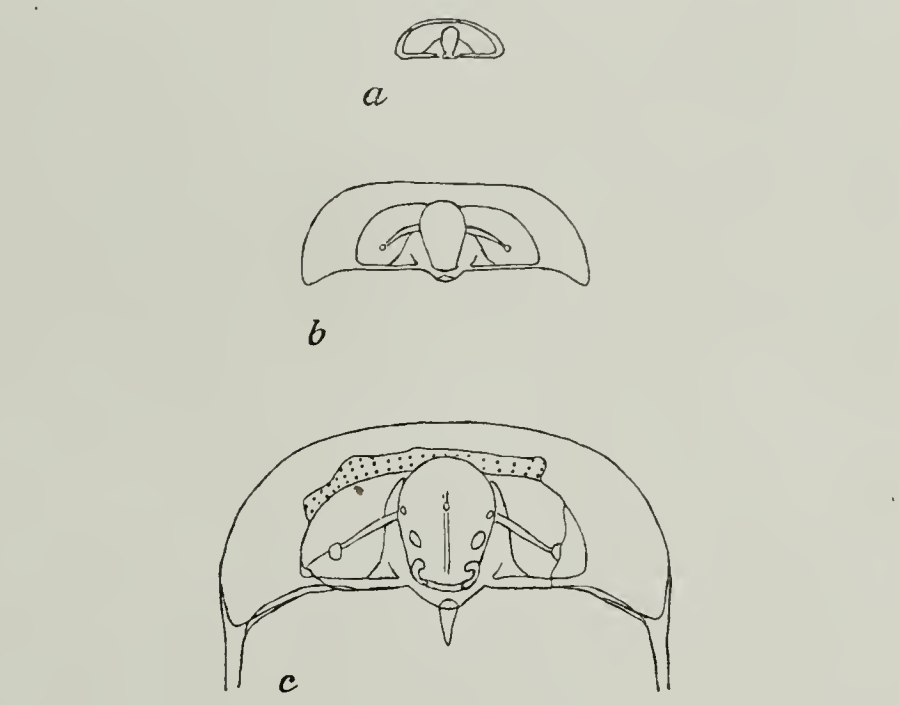


Fig. 20. *Reedolithus carinatus* (Ang.). × 7.5. Shapes in the development of cephalon. $a-d$ = H 514, H 518, H 516, H 451. From ampyxlimestone. a from Gomnæs, d Gullerud, Ringerike, b, c Huk, Oslo. (Brøgger, Kiær coll. Pal. Mus. Oslo). Outline restored.

per, but are easily separable from the steeper central portion of the glabella.

The ontogeny shows that the triangular fields found in the youngest Meraspid stages of the subfamily Trinucleidae, and compared by BEECHER (1895) with the similar alae of Harpedidae, during the stages of growth are assimilated by the glabella, forming the lateral lobes of glabella. The question of the course of the axial furrows and the bounding of the glabella will be discussed in the chapter on the ontogeny of *Tretaspis* p. 65.

Cheek lobes are not very much changed during the ontogeny. The breadth decreases. This is the result of an increase of breadth near the occipital ring. In the youngest stages the lobes are rather flat with a steeper portion against the fringe, resembling *Trinucleus foveolatus*.

The lateral eye tubercles with eye lists are as above mentioned found already in the stages of 0,85 mms cephalon length.

In the earliest stages (Pl. 4, Fig. 4) the eye lists are short. During growth the length increases and the small eye tubercles are placed near the genal angle. The eye lists are very distinct. The broad inner portion traverses the axial furrows on the internal cast. (Pl. 5, Fig. 5). In the latest stages the eye tubercle obtains an unusual size. It maintains the posterior lateral portion. In some cases (Pl. 4, Fig. 10) a more anterio-medial position of the eye tubercle is indicated.

The fringe has been briefly described in the youngest stages. The specimen H 518 (Pl. 5, Fig. 1) gives good details of the fringe. Fig. 18 shows the arrangement of pits. Sulci only occur in the inner row where new rows of pits are developed. Anterior alternating rows of pits are found. Laterally the irregular arrangement of pits shows a resemblance to the arenig *Cryptolithus primitivus* KLOUČEK, Fig. 35, p. 82. On Pl. 4, Fig. 8, details of fringe are preserved from a cephalon of about 1,4 mms length. Near the margin large pits in more or less radial sulci are found. The sulci probably represent a division of pits.

The later stages have a distinct concentric arrangement of pits; more or less assymetric. In the large specimens an average type of pit arrangement can be determined in spite of the individual variation. On the fringe two outer and two—three inner concentric rows are more symmetrical than those between. A radial symmetry is often prominent in the outer and inner rows. The characters are seen on H 441 (Pl. 5, Fig. 5—7) and Fig. 17. The innermost row seems to be developed in a cephalon length of about 2,2 mms. The outer and inner rows of pits were probably developed at a rather late stage. As in *Tretaspis* we probably have a division of pits, through radial sulci, in the marginal und the inner row.

The shape of the fringe changes through the range of development. Fig. 19 gives us an idea of the shape in 7 stages from the smallest to the largest known specimen. The smallest specimens (Fig. 19, b—c) have a very flat fringe. The rather broad posterior portion (Pl. 5, Fig. 1) and the

anterior portion taper very slightly from the cheek-lobes and glabella. During the later stages up to a cephalon length of about 2,5—3,0 mms, the fringe maintains the rather flat surface. (Fig. 18, d, e). Genal prolongations are a little more prominent (Pl. 5, Fig. 5—7). In the later stages the shape of fringe is much changed (Fig. 18, f, g). The fringe surface, which in the younger stages was rather flat, usually becomes concave near the margin, forming a distinct brim as in the genus *Tretaspis*. On the brim pits are often placed in radial sulci as in *Tretaspis* (Pl. 4, Fig. 9, Pl. 5, Fig. 13). The inner part of the fringe, the cheek roll, becomes very steep. In some cases the angle of declination is about 80°. The outline of fringe, which in the younger stages was nearly semielliptic, becomes semicircular with more prominent genal prolongations. The outline of fringe is drawn in Fig. 20.

The above described development of the different morphological characters does not quite follow the size of the cephalon. The strongly carinate glabella might e. g. occur in large specimens in some cases (Pl. 5, Fig. 9), but this must only be explained as individual variations.

Barrande (1852) found that the stage with 6 segments of thorax in *Cryptolithus ornatus* is reached at a cephalon length of 2,5 mm.

In *Tretaspis* the stage is reached at a length of about 2,5 mm.

The different Meraspid stages cannot be determined in *Reedolithus*, but they are, compared with the above-mentioned genera, surely finished at a cephalon length of 2 mm. (St O had a length of cephalon of 0,45 mm in *Reedolithus* and about 0,55 mm in *Tretaspis*).

The ontogeny of *Reedolithus carinatus* shows some characters different to other known genera of Trinucleidae.

Greater changes in the morphological characters are found down in the latest stages of growth.

From the ontogenetic description a marked change is indicated by the stage represented by a cephalon length of about 2,5 mms.

The younger stages are characterized by: Very strong, elevated, carinate glabella without distinct glabellar furrows. Flat fringe with a small angle of declination. No distinct brim.

The older stages: Broader and less elevated and less carinate glabella having distinct glabellar furrows. Fringe steep, concave at the margin forming a brim.

In the ontogeny two different stages or groups can be separated in the later stages of the ontogeny.

The latest group shows great resemblance to the earliest *Tretaspis* occurring in somewhat younger layers *Tretaspis cerioides* var. *angelini*. As will be discussed later, p. 83 the latest stage probably represents a convergence to the genus *Tretaspis*. The occipital spine however is maintained.

Genus *Cryptolithus* Green (p. 15).

Cryptolithus dicors, (Ang.).

1851 – 54, *Trinucleus dicors* Angelin p. 84, Pl. 40, Fig. 28.
1929 , *Reuscholithus reuschi* Bancroft, p. 82, Pl. 1, Fig. 3, 4.

Distinguishing characters. "Cephalon broad. Surface of glabella and cheek lobes with finely-meshed reticulation. Fringe narrow. Four concentric rows of pits anteriorly. The two marginal rows having small, more or less intercalating, irregular pits. Number exceeding that in the inner rows. Numerous small pits on the innermost rows of lateral portion of fringe. Lower lamella with two rows of intercalating pits without the girder."

The description of Angelin is very brief. Its illustration gives a good idea of the cephalon without fringe. The fringe is drawn in a lateral view, but the characteristic arrangement of pits is not noticeable. The original of Angelin from Norway is lost, but there seems to be no doubt that the material present belongs to the species described by Angelin. A good collection of this form has been made in Norway by G. Holm. It belongs to the Riksmuseum in Stockholm. One of his specimens Ar. 2293 has been chosen as a neotype.

General description. Cephalon of semicircular outline. Glabella strongly arched, without carina. The median line of glabella from the top backwards to the occipital furrow appears in lateral view as a straight line. No pseudo-frontal lobe developed. Median tubercle present (Pl. 6, Fig. 9). Surface of glabella shows a finely-meshed reticulation ranging from the anterior portion backwards to the occipital furrow. The steep lateral portions of glabella smooth.

1rst pair of glabellar furrows obsolete. 2nd pair faint, noticeable in some specimens (Pl. 6, Fig. 8). 3rd pair well marked laterally. The furrow consists of a distinct lateral pit and a faint furrow going anterio-medially. In some cases all these pairs of glabellar furrows appear very distinctly as dark spots against the lighter, surrounding surface of shell. Similar spots are found in *Reedolithus* and *Tretaspis*, and are further discussed on p. 94. Occipital furrow has a lateral pit comparable with that found in 3rd glabellar furrow. Occipital ring broad, furnished with occipital spine. The character of it has not been elucidated. Axial furrows distinct and shallow. Antennuary pits present.

Cheek lobes with a flat posterio-medial portion. Surface shows a very fine round-meshed reticulation. The steeper portion of the cheek lobe near the fringe is smooth. Smooth surface is also found near the posterior portion of glabella. A distinct occipital furrow bounds the narrow occipital segment.

In a small specimen (Ar. 2305) length = 2,5 mm (cephalon) traces of eye-lists were found near the axial furrow. Adult specimens quite lack lateral eye-lists.

Fringe, like glabella, has typical *Cryptolithus* characters. Breadth smallest in front, but only a little larger laterally, without the posterio-lateral portion. which has a prominent breadth. Faint genal prolongations. Surface of upper lamella flat. Some specimens show a concave fringe in front.

Pits small, corresponding in both lamella. They appear as hollow pillars, of "hourglass" shape. No "rounded boss or mamelon" mentioned by Reed (1912, p. 399) is found. Pits of different size are found. Pl. 6, Fig. 10 shows small pits in the outer and inner rows and larger in the middle. On Pl. 6, Fig. 7 a division of pits in the lateral part of the outer row is indicated. A new row arises. The sulci are not radial and thus give rise to a new concentric row different to that found in *Tretaspis* where the division of pits into a new row is made through radial sulci.

The number of pits in the marginal row is prominent, about 65—70. The next row lies close to it with partly intercalating pits. (Pl. 6, Fig. 1, 8). The two rows are probably developed from one row as above described. This is also indicated in the larval stage (see below). Lower lamella seldom found in the right position below the upper lamella. It is usually broken off. Lower lamella with prominent girder anteriorly, less distinct posteriorly. It bounds the outer band with a double row of pits. (Pl. 6, Fig. 2, 11, 12). The two rows of small irregularly arranged, or intercalating pits fully correspond to the same on the upper lamella. Within the girder two concentric ridges, secondary girders, are found (Pl. 6, Fig. 2). In front two rows of pits are found on the inner band, laterally more rows are developed.

Thorax unknown.

Pygidium known from 3 well preserved specimens (Pl. 6, Fig. 3, 10). Length about 1:3 of the breadth. Outline of pygidium subtriangular. Posterio-lateral outline gently arched especially in the anterior portion. Surface of shell smooth except the posterior band which is pierced by terrace lines. Rachis narrow, bounded by shallow, distinct, axial furrows. Breadth of rachis gently decreasing posteriorly. Rachis contains a number of segments. In the anterior segments the impressions of appendifers very distinct. The two specimens depicted (Pl. 6, Fig. 3, 10) have 14 and 17 appendifers corresponding to appendages on the lower side. In cephalon 5, and in thorax 6 appendages are known. The total number of appendages must have been:

Specimen	Cephalon	Thorax	Pygidium	Tot. number
H 364	1 + 4	6	17	28
H 363	1 + 4	6	14	25

For comparision the lower side of *Cryptolithus tesselatus* GREEN restored by RAYMOND is reproduced Fig. 39 b, p. 95.

The figure of RAYMOND shows 23 appendages, a number corresponding fairly well with those found in *C. dicors*.

Pleura of pygidium well marked, diverging almost radially from the anterior median part of rachis. Median part of pleura gently arched. Posterior portion of pygidium bent down at an angle of 90° forming the posterior band.

Larval stages are found in a few specimens. Pl. 6, Fig. 5 shows the lower lamella in ventral view of an early Meraspid stage. Lower marginal rim is prominent, forming a "pseudo-girder". No division has taken place in the row of pits on the outer band. Compared with the known stages of *Cryptolithus* and *Tretaspis* the specimen probably represents St. II.

Pl. 6, Fig. 6 shows a young pygidium. Posterior line arched. Rachis unusually arched, not separated from the pleura by distinct axial furrows. 4 segments visible.

BANCROFT (1929, p. 83) has described some Meraspid stages.

Dimensions. Max. length of cephalon 9 mm, breadth 22 mm. Max. length of pygidium 7 mm, breadth 23 mm.

Occurrence. The species only known from Norway and England. In Norway it is found in the upper Chasmops limestone at Nakholmen near Oslo and at Ringsåsen, Ringerike. The age is probably the transition beds from Caradocian to Ashgillian.

Affinities. Most species of *Cryptolithus* described have been badly preserved. The surface of shell can therefore not be used for classification. *Cryptolithus dicors* (ANG.) differs from the Bohemian species: *C. goldfussi* (BARR.), *C. ornatus* (STERNB.) and *C. ultimus* (BARR.). BARRANDE 1852, Pl. 29—30), by the numerous irregularly arranged pits. *C. greenieri* (BERGERON) (1894, p. 42) shows resemblance in the narrow anterior fringe, indications of numerous pits in the marginal row, but the characteristic double row of pits in *C. dicors* is not present.

C. nicholsoni REED (1910, p. 212, Pl. 16) resembles the species described, but differs in the prominent radial arrangement of pits. *C. gibbifrons* (McCOY), (REED, 1914, Pl. 29, Fig. 5—7) has more prominent glabella and radial arrangement of pits which are partly sunken in radial sulci in front.

C. tesselatus (GREEN) does not seem to be a clearly defined species. REED (1912, p. 387) describes the arrangement of pits on the fringe of this species. His figures of the fringe of this species from Shropshire (1914, Pl. 29, Fig. 3) show a resemblance to *C. dicors*. The marginal row of pits has smaller and more pits than the two rows within. On the lower lamella the girder is found within the second row of pits, not within the

first row as indicated by RAYMOND in his restored figure (1920, Pl. 63, Fig. 20) (copied p. 95, Fig. 39b). Of those described by REED *C. dicors* shows the greatest resemblance to the specimens from Onny River, Shropshire, by the intercalating pits. They differ in the lack of the typical double row of small pits near the margin. The posterio-lateral portion of fringe is broader in *C. dicors*. *C. caractaci* (MURCH.) differs from the species by a smaller number of rows of pits in front (MURCHISON, 1839, Pl. 23, Fig. 1 b).

The different species of Cryptolithus have not been fixed by definite specific characters. It is very difficult to give a sufficient decision of the affinities of a species as long as the earlier descriptions do not give distinct limits of variation of the different species. BANCROFT (1929) has described a number of new *Cryptolithus*. *Cryptolithus (Reuscholithus) reuschi*, BANC. seems to be identical with the present species.

Cryptolithus cfr. *portlocki* (SALTER.).

Pl. 6, Fig. 13.

Distinguishing characters. "Fringe with 3 concentric rows of pits in front and 4—6 laterally. Outer row with more and smaller pits than the other. A concentric ridge within the outer row of upper lamella."

In the sandy layers from the uppermost part of Ordovicium in the Oslo district, 3 specimens of *Cryptolithus* are found.

General description. The impression of glabella shows a Cryptolithus shape without the glabellar furrows.

The fringe is better preserved. The upper lamella flat, rather narrow in front and broad laterally with little posterior prolongation of the genal angle.

The marginal row of pits has smaller and more pits than the other rows. A concentric ridge is visible within the outer row of pits. The pits are arranged in concentric rows. A radial symmetry might be found in the rows within the marginal one. Anteriorly 3 rows of pits are found. Laterally the inner rows divide and the number becomes 4—6 and 9—10 at I.

The lower lamella shows the same arrangement of pits. Girder within the 1rst row of pits rather prominent. Secondary and tertiary "girders" are indicated.

Dimensions: Length of cephalon = 9,5 mm, breadth 22 mm.

Occurrence. The specimens are found on Husebergö and N. Langö near Oslo. The species occurs in the uppermost part of Ordovicium in the upper Chasmops zone together with *Tretaspis latilimbus* LINRS.

Affinities. The described species shows the greatest resemblance to *Cryptolithus portlocki* (SALTER). The species has only been reckoned as a variety of *C. tesselatus* (= *concentricus*) by some authors, SALTER (1853),

Fearnsides, Elles and Smith (1906—1907). The classification does not seem to be quite established. The specific characters are in several cases of little systematic value. *C. portlocki* from Ashgillian in Tyrone, Ireland (Fearnsides etc. 1906—1907, Pl. 8, Fig. 1—2) shows resemblances to the present species. The number of pits in front is the same, but the concentric ridge is absent and the shape of the lateral portion of the fringe is rather different. *C. tesselatus* (= *concentricus*) described by Reed from middle Bala (Caradoc) (Reed, 1912, Pl. 18, Fig. 4, 7—12) differs from the present species in having more rows of pits and the girder situated within the second row of pits. In the paper of Bancroft (1929) the youngest species show the greatest resemblance to the present form.

Cryptolithus sp.

Pl. 6, Fig. 14.

From Fjecka in Dalarna, Sweden, some specimens are present which belong to this genus, but cannot be further determined. The shape of glabella, the lack of distinct lateral furrows and the concentric arrangement of pits on the fringe show the genus *Cryptolithus*. The lower lamella is preserved. 2 rows of pits are found without the girder. This indicates a relationship to *C. tesselatus* var. *caractaci* (Murch.), Salter (1853, p. 6) = *C. tesselatus* Green, Reed (1912, p. 387, Pl. 8, Fig. 4, 7, 12). The species is most allied to the Bala (Caradocian) species of *Cryptolithus*. It differs from *C. dicors* (Ang.) which has smaller pits.

Dimensions: Length of cephalon about 10 mm.

Occurrence: In the "Bryozoic beds" below the black shales with *Tretaspis seticornis* in Dalarna. The age is probably Caradocian.

Genus *Tretaspis* Mc'coy (p. 15).

Tretaspis cerioides (Ang.)

Pl. 9, Fig. 1—4.

Trinucleus cerioides Angelin 1851—54, p. 65, Pl. 34, Fig. 2--26.

Distinguishing characters. "Glabella with distinct pseudofrontal lobe. Surface of glabella and cheek lobes strongly reticulate. Fringe broad anteriorly with small genal prolongations. Upper lamella having 2—3 rows of pits of which the 3rd is scarcely visible lying in radial sulci, and 3 rows on the cheek roll. Posterior margin with 7—8 pits. Lower lamella with 1—2 rows of pits outside a short girder, 4—5 rows in radial sulci within. Variation in the number of pits seen on the graph Fig. 21."

Angelin states the Regio Ba as the horizon where this species occurs. This indicates lower layers than those with *Tretaspis secticornis* and *T. granulata*. The age would correspond to the Chasmops layers in Norway.

When examining the Swedish collections in Lund, Uppsala and Stockholm no specimens from ANGELIN were found. In the Riksmuseum in Stockholm some specimens are present found in the Beyrichia limestone in Vestergötland which are rather like the drawing of ANGELIN.

On account of the scanty Swedish material I have chosen a neotype among the Norwegian specimens (H 381) which shows both lamella of the fringe.

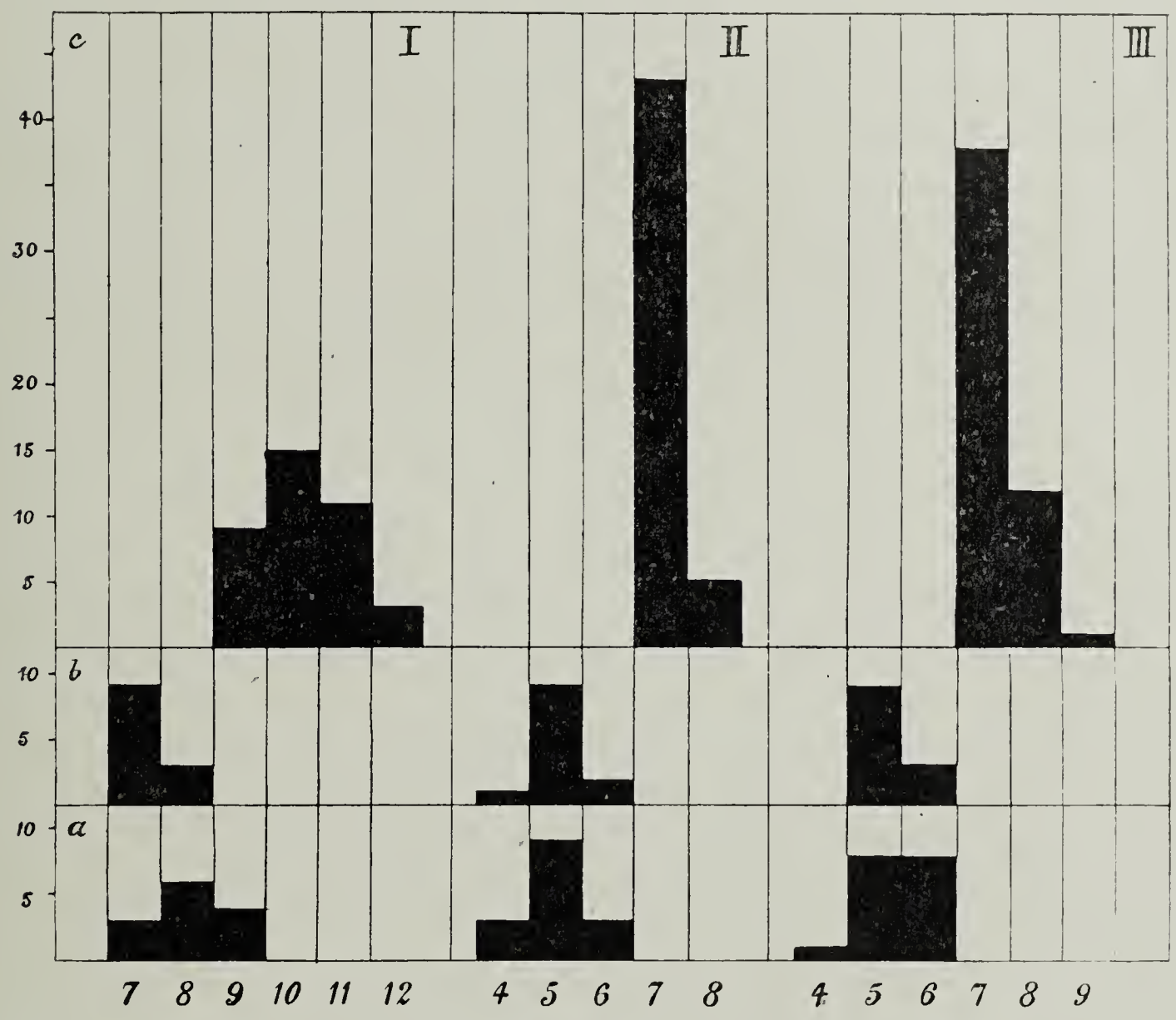


Fig. 21. Variation in the number of pits on the fringe of early Norwegian *Tretaspis*. *a*. *T. cerioides* (ANG.) var. *angelini* n. var. from upper Chasmops limestone near Oslo. *b*. *T. cerioides* (ANG.) from upper Chasmops limestone Ringerike. *c*. *T. kiæri* n. sp. from lower Trinucleus limestone, Ringerike. Explanation and discussion of the graphs p. 10.

As is common among the species of *Tretaspis* the surface of the shell is seldom visible. In one case the surface has been prepared (Pl. 9, Fig. 3).

General description. Outline of cephalon semicircular. Genal spines gently divergent. Glabella strongly arched with distinct semispheric pseudo-frontal lobe, hiding the anterior fringe. Surface of glabella strongly reticulated on the pseudo-frontal lobe and medial posterior portion of glabella. The strong reticulation is the reason why the upper surface of shell is very seldom found. The shell breaks off from the stone along the lower, rather smooth surface. Usually only internal casts are found. Pl. 9, Fig. 3 shows a specimen where the reticulated surface has been prepared.

The reticulations consist of a network of fine, raised lists. The nearly circular or hexagonal fields between have a flat base. No traces of openings can be found in the fields. Median tubercle is badly preserved in the test specimen. Only a raised base in the reticulation is visible. The internal cast carries a distinct tubercle indicating the usual thin test.

1rst glabellar furrow nearly absent, only visible on internal casts forming a small round impression. 2nd strongly developed of rectangular shape. Beginning within the axial furrow passing medio-posteriorly separating the pseudo-frontal lobe from the posterior portion of glabella. The furrow deepest anteriorly having a rather flat base. 3rd glabellar furrow strong, passing medio-anteriorly. The lateral part communicates with the lateral sulci in the occipital furrow.

Lateral lobes smooth, well-marked from the axial furrows. Axial furrows distinct with antennuary pits. Occipital ring broad without occipital spine.

Cheek lobes strongly arched having a coarse reticulation. Lateral eye tubercles very distinct. resembling those found in *T. kiæri*. Eye lists faint. Occipital segment with a strong lateral portion forming a marked support to the posterior portion of fringe.

Fringe of a typical *Tretaspis* character. In dorsal view the fringe is scarcely noticeable on account of the steep inner portion. This causes great difficulties in the illustrations of the species of *Tretaspis*.

Fringe of equal breadth round the cheek-lobes except the genal prolongations which show faint increase in breadth.

The posterior prolongation of fringe from the front of the first thoracic segment only represents one half of the breadth of the fringe.

The upper lamella of fringe is divided into an upper convex part, the cheek roll, and a lower concave part, the brim. The division is not very prominent in this species. The brim is little developed as in *T. latilimbus* (Pl. 9, Fig. 1—3). Pits rather large. The arrangement of pits can be studied on Pl. 9, Fig. 1 *b—c*, 3. Near the margin a row of deep radial sulci is found. The bottom of the sulci usually contains 2—3 rows of pits. If 3 are present, the two marginal rows lie quite close together. On the cheek roll 2—3 rows of pits occur. The rows are separated by raised concentric lists (p. 103) (Pl. 9, Fig. 3). They are not present on the lower surface of the lamella, on the internal cast. The rows on the cheek roll have certainly been developed by division of pits in radial sulci. When 3 rows are found the two innermost rows fuse together laterally. All transitions are found, from a single row of pits to two pits in radial sulci, to two separated rows of pits to two rows separated by a concentric reticulating list. According to the graph Fig. 21, 7—8 pits are found at the posterior margin (I). A minute study of the surface of the shell of fringe shows small granulæ distributed between the pits. They are most common near the outer margin. Similar shapes are found in *T. seticornis* (p. 100). No opening at the top of the granulæ can be recognized.

Marginal suture situated on the nearly vertical marginal band. The suture is beautifully preserved in several specimens from Norderhov, Ringerike. It is marked by a narrow, raised line, or by a faint fissure. In some instances a very fine break line can be traced. By pressing a fine needle on the surface of the upper lamella near the margin, the upper lamella easily splits off along the marginal suture. The marginal suture will be discussed in a special chapter on p. 92.

Lower lamella usually found in right position to the upper lamella. On the lower marginal band and rim small points and granulæ are found corresponding to those found in *Tretaspis seticornis* and explained (p. 100) as canal openings.

Outer band very distinct, tapering slightly towards the margin. In front view the margin is bent up in front, forming an arc. The base of genal spines is also elevated as compared with the low lateral portion of fringe. Similar shape of the cephalon outline is found in *Limulus*. On the outer band one row of pits is usually present. Pits often radially divided in very short sulci with two pits, corresponding to the arrangement on the upper lamella. The outer band continues posteriorly in the genal spines. Genal spine with a right angled triangular section. The right angle corresponds to the continuation of the girder. A prominent girder found within the outer band (Pl. 9, Fig. 1 d), girder angle about 90°. Lower surface pierced by terrace lines. 4—5 rows of pits on inner band sunken in deep radial sulci. The outermost row corresponds to the inner row in the radial sulci on upper lamella. Upper portion of inner band bent down, forming a broader concentric list serving as an integument attachment.

Thorax only found in one enrolled specimen from Bjerkö, Asker. Details not known.

Pygidium: Only the small pygidium Pl. 9, Fig. 4 was found. Posterior margin of semi-elliptic outline. Rachis with 4 visible segments. The first segment consists of two rings. Pleural fields rather concave with 3 transverse ridges representing the pleuræ.

Larval stages have been found. A cephalon (Pl. 9, Fig. 2) measuring 1,4 mm shows several characters differing from the adult. Glabella strongly convex with carina. Trace of rather large median tubercle. No pseudofrontal lobe. 1st pair of glabellar furrows scarcely visible, 2nd pair visible, transverse, gently posterio-medial. 3rd pair visible, transverse, gently anterio-medial. Lateral lobes rather flat, separated from glabella. Cheek lobes broad with well developed lateral eye tubercles and eye lists. Faint genal prolongation of fringe. Fringe resembling the adult, 2—3 pits in sulci in front, with 2 rows on the cheek-roll. The age of the specimen probably corresponds Meraspid stage III. Cephalon H 369 of length 2,5 mm shows a prominent brim. It indicates a relationship to *T. kiæri*.

Dimensions. Average length of cephalon = 6,5 mm, breadth = 13,5 mm. Average dimensions of pygidium unknown.

Occurrence. The species occurs in the upper part of upper Chasmops limestone at Norderhov, Ringerike, and Bjerkö, Asker by Oslo. The age of the layers is discussed on p.

Affinities. *Tretaspis kiœri* is closely related. It differs in the larger size and the greater number of pits on the fringe. Three well separated rows of pits are found in the radial sulci on the upper lamella. The larval stages of *T. cerioides* also suggest the close relationship of the two species. The species differs from *T. seticornis* which has fewer pits and broader, nearly smooth glabella. *T. latilimbus* and *T. granulata* have a greater number of pits.

Tretaspis cerioides var. *angelini* n. var.

Pl. 9, Fig. 5—10.

Distinguishing characters. "Pseudo-frontal lobe of glabella slightly developed. Glabellar furrows in rather transverse position. Reticulation distinct, but with rather low lists. Fringe with shallow pits. Arrangement as in *T. cerioides*."

Found in the layers of the same age as those containing *T. cerioides*. The species and the variety have not been found together. They probably replace each other.

General description. Glabella rather broad, anterior portion hiding the anterior fringe. Pseudo-frontal lobe not well marked. Surface reticulated, but not as strong as in *T. cerioides*. Glabellar furrows indicate primitive characters. 1rst furrow of usual shape. 2nd and 3rd pair more transverse than is usual in the members of the genus *Tretaspis* (Pl. 9, Fig. 10). They show resemblance to the glabellar furrows of *Trinucleus foveolatus* and of the younger stages of *Tretaspis*. Antennuary pit, 3 glabellar furrows and the pits of the occipital furrow lie in one straight line with about the same intervals. This makes it hard to assume a reduction of one antenna between the antennuary pit and the 1rst glabellar furrow (cfr. p. 94). Cheek lobes rather flat with low, but distinct reticulation (Pl. 9, Fig. 5, 10). Lateral eye tubercles small, but strongly elevated. Eye lists faint, best marked on the internal casts.

Fringe shows the same general characters as *T. cerioides* in the arrangement of pits. It differs by its constant shallow pits and marginal sulci (Pl. 9, Fig. 5, 10). In one specimen (Pl. 9, Fig. 10) the radial sulci on the upper lamella are nearly quite reduced. Girder very strong (Pl. 9, Fig. 7) having terrace lines. Deep radial sulci on the inner band. The sulci become reduced posteriorly near the genal spine.

Thorax unknown.

Pygidium. Posterior outline oval. Rachis contains 5 segments, determined by the corresponding appendifers. 3—4 pleurae are indicated.

Larval stages. From Terneholmen some Meraspid stages have been found. Pl. 9, Fig. 8 shows a dorsal fringe with three rows of pits anterio-laterally. The 2 outer rows lie in very faint radial sulci, but the inner row is separated by a concentric list. Length of cephalon 0,9 mm. Compared with *T. seticornis* this stage probably represents Meraspid st. I. In *T. seticornis* st. I has two rows of pits (Fig. 29). *T. cerioides* var. *angelini* has the outer row divided into two rows. Pl. 9, Fig. 6 a—b depict a specimen of cephalon length = 1,45 mm. It probably belongs to St. II. Glabella strongly arched, carinate, lacking pseudo-frontal lobe. 3 pairs of faint glabellar furrows in transverse position. Median tubercle prominent but not well marked. Faint reticulation anterio-medial to the tubercle.

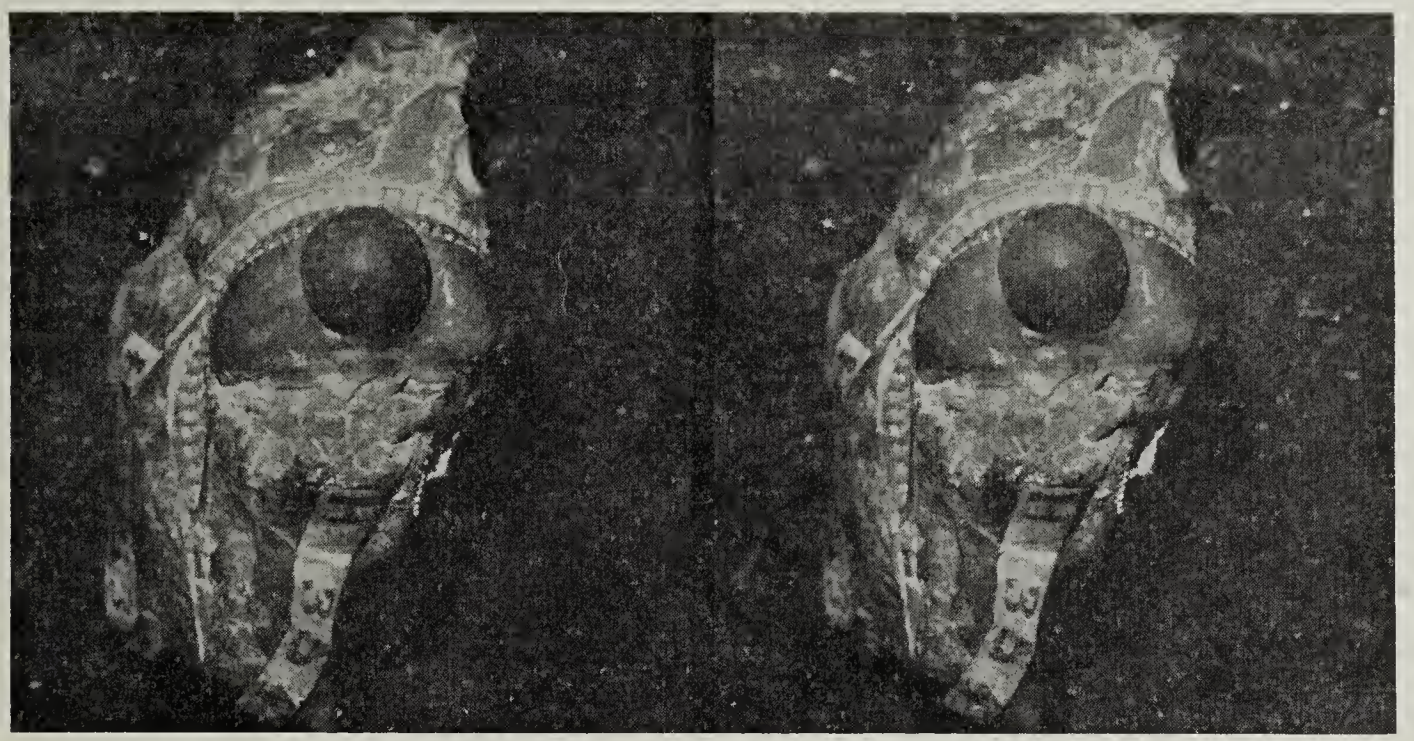


Fig. 22. *Tretaspis kiæri* n. sp. × 2. Stereoscopical photo. Lower Trinucleus limestone Frognø, Ringerike (H 353, Kiær coll. Pal. Mus. Oslo).

Cheek lobes with well developed lateral eyes and eye lists. Fringe with steep cheek roll and flat brim. Brim with radial sulci containing 3 rows of pits. Two rows of pits within the sulci separated from the sulci by a concentric list. This stage has probably developed from the earlier, described above, by a division of the outer and inner row of pits. In St. II of *T. seticornis* four rows of pits are found. The great number of pits in the present form seems to be indicated at an early stage of development.

Dimensions: Average length of cephalon 4,5 mm. Largest specimen measured: 7 mm. Average breadth 9— 10 mm. Average length of pygidium unknown.

Occurrence. In the highest beds of upper Chasmops limestone on the islands Nakholmen and Terneholmen near Oslo. *T. cerioides* was found somewhat far to the west and north in the Oslo field.

Affinities. The above described form shows a resemblance to *T. cerioides*. The general shape of the fringe with the arrangement of pits

is the same. This character is easy to determine. The shape of glabella and glabellar furrows depends to a great extent upon the kind of preservation, and are thus difficult to compare with other worsely preserved specimens. The shape of glabella, with the faint pseudo-frontal lobe differs from *T. cerioides*. The weaker reticulation, the shallow pits and shallow radial sulci on the upper lamella are also different to the species. These differences make it necessary to establish a new variety. The possible primitive character of glabella indicates a new species, but the close resemblance of the fringe of *T. cerioides* makes it most natural to determine it as a variety of that species. The differences from the other species are nearly the same as in *T. cerioides*. The variety, however, shows more resemblance to *T. latilimbus*.

Tretaspis kiæri n. sp.

Pl. 10, Fig. 1—6, Pl. 11, Fig. 12, Pl. 13, Fig. 13, Pl. 14, Fig. 1—3.

Distinguishing characters. "Glabella prominent, semispheric pseudofrontal lobe with strongly reticulated surface of shell. Cheek lobes reticulated. Fringe steep, broad anteriorly. Upper lamella with radial sulci containing 3 rows of pits on the brim, 4—5 rows on the cheek roll. Lower lamella with two rows of pits on outer band. 5—6 rows of pits in radial sulci on the inner band within a well-marked girder. About 9—12 pits along the posterior margin of fringe. Pygidium with rather narrow rachis holding about 7 segments."

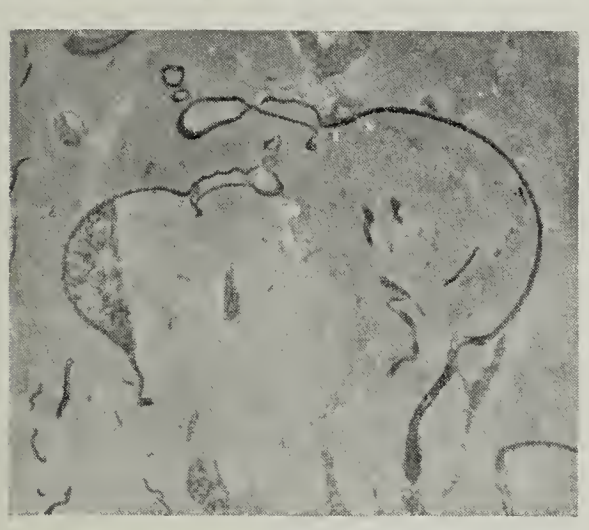
In the lower Trinucleus-limestone at Frognø, Ringerike, Prof. J. Kiær discovered a rich fauna with numerous beautifully preserved specimens of a *Tretaspis*. The fossiliferous bed was only found in a limited locality. The trilobites with white shell are easily distinguishable from the grey limestone. The interior of the bulbous portions of cephalon as f. inst. glabella is often filled with calcite, indicating a filled cavity probably caused by putrifying gases. Of the cephalons almost only internal casts are preserved on account of the strongly reticulated surface of glabella and cheek lobes, and the concentric lists of fringe which have been nearly impossible to prepare out of the limestone. To get a right impression of the structure of

Fig. 23. *Tretaspis kiæri* n. sp. × 3,3. Serial sections. Longitudinal section near the median cephalon. The double nature of fringe may be studied. *gl* = glabella, *glf* = glabellar furrow, *g* = girder, *u. l.* = upper lamella *l. l.* = lower lamella. Distances between the sections: 0,09, 0,09, 0,09, 0,12 mm. Lower Trinucleus limestone Frognø, Ringerike. (Kiær coll. Pal. Mus. Oslo).

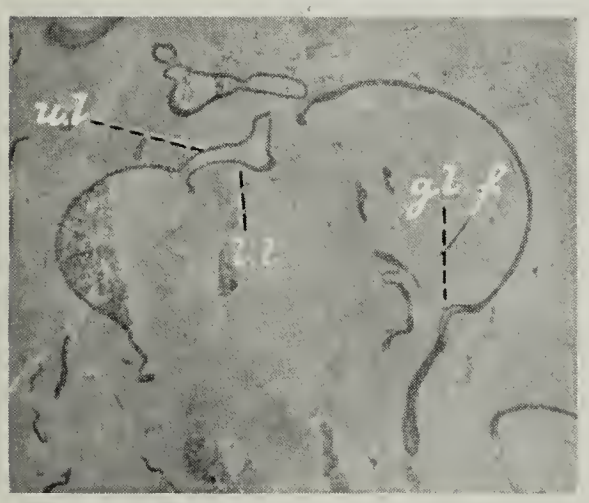
Fig. 24. *Tretaspis kiæri* n. sp. × 3,3. The same series ot sections. The biggest specimen is cut across the cheek lobe with the lateral eye tubercle. The smaller specimen shows the lateral portion of fringe. *mgs.* = marginal suture. *i. a.* integument attachment. *l. e.* = lateral eye tubercle. *g* = girder. Distances between the sections: 0,11, 0,20, 0,10, 012 mm.

A 1

A 2



A 3



A 4

A 5

Fig. 23.

Fig. 23 (cp. page 50, below).

A 39

A 40

A 42

A 43

A 44

Fig. 24.

Fig. 24 (cp. page 50, below).

the surface of cephalon and the lower surface of lower lamella, several thin sections have been made (Pl. 14). A good illustration has been obtained by serial sections of succesive grinding. 70 photos have been taken, with the distance of each grinding measured. Samples of the serial sections are depicted in Fig. 23—25.

It is difficult to get a right impression of the strongly arched cephalon of *Tretaspis* in the usual illustrations. In dorsal view the steep fringe is quite hidden. A stereoscopic photo made by curator A. Heintz of the Pal. Mus. is depicted in Fig. 22 to show the right shape.

General description. Cephalon with semicircular anterior outline. Genal angles posteriorly prolonged. Glabella prominent. Strong, nearly semispheric pseudo-frontal lobe. (Fig. 23).

Surface strongly reticulated. (Pl. 14, Fig. 1, 2 and text Fig. 23). The reticulation closely resembles *T. cerioides*. Meshes largest near the top of glabella, are lacking laterally, posterior to the pseudo-frontal lobe. The lower surface of the shell of glabella not quite smooth, but supplied with small granulae, or grains. The lower surface beneath the glabellar furrows quite smooth as in other genera and species of Trinucleidae. On the internal cast a distinct median tubercle. A faint median list posteriorly and two anterio-laterally from the tubercle, indicated as in *T. seticornis* Fig. 40 p. 96. The nature of the lists discussed on p. 96. Median tubercle visible on the upper surface of test (Pl. 13, Fig. 3). Three pairs of glabellar furrows. 1rst pair nearly reduced, situated near the rise of the eye-lists. 2nd pair very distinct, bounding the posterior portion of the pseudo-frontal lobe, ovoid shaped, deepest in front, nearly transverse, with the median portion a little more posterior. 3rd pair oblique, forming an angle of 45° to the median line. The furrows bounded laterally by the axial furrows. Lateral lobes only slightly developed. Occipital furrow very broad in median part, laterally two deeper pits corresponding to the lateral portions of 3rd pair of glabellar furrows. No occipital spine or tubercle found. Axial furrows broad. Antennuary pits well developed. Cheek lobes arched, anterior and lateral portion against fringe very steep.

Large lateral eye tubercle strongly elevated. The tubercle is visible on the sections Fig. 24. Eye lists only visible as faint ridges on the internal casts. In some specimens (Pl. 10, Fig. 1) genal cecae are seen from the tubercle to the genal angle. Usually two branches in the lateral portion. Fringe almost only known from internal casts. One specimen (Pl. 11, Fig. 12) has preserved the upper surface of the shell of the margin, the structure of fringe may be studied in the serial sections Fig. 25, and on Pl. 14, Fig. 1—3.

The shell structures are discussed in later chapters p. 96.

Upper lamella with steep cheek roll tapering at an angle of about 80°. Rather convex anteriorly, flat laterally. Brim below cheek roll broad, concave. The internal cast of upper lamella depicted Pl. 10, Fig. 3, 6.

Pits large. On Pl. 10, Fig. 3 b, the shell is present in the bottom of the pits. A small black spot indicates a hollow pillar.

The arrangement of pits varies to a certain degree. Within several specimens an assymetric arrangement is found. (Pl. 10, Fig. 6). The specific variation is seen in the graph Fig. 21.

On the concave brim deep radial sulci, having 3 distinct well separated rows of pits. Laterally the inner row passes out from the sulci, leaving only two rows.

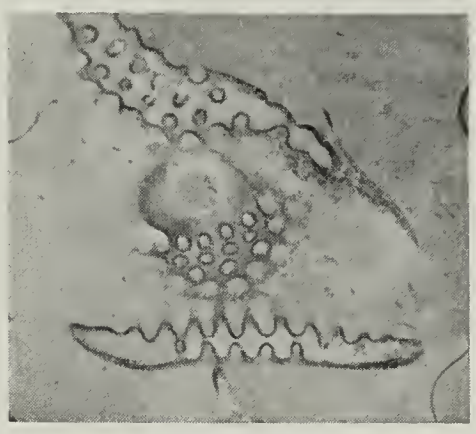
On the cheek roll 4—5 concentric rows of pits radially arranged. The radial lines of pits usually point between the radial sulci on the brim. The number of pits in the rows on the brim a little smaller than in the rows on the cheek roll. The two inner rows often show pits lying in radial sulci indicating development of rows by division of pits. This is common anterior to the dorsal furrows. Between the rows of pits on the cheek roll concentric lists are found (Pl. 14, Fig. 1).

Genal prolongations with more rows of pits. Along the posterior margin (I) 9—12 pits are found. (Fig. 21).

Lower lamella, depicted in Pl. 10, Fig. 5, 6, is divided by a prominent girder in an outer and inner band. Girder with terrace lines. Terrace lines also found on outer band. Outer band with two rows of pits corresponding to the two marginal rows in the sulci on upper lamella. Faint radial sulci sometimes indicated. Laterally the outer band shows a declination to the margin. Inner band with 5—6 rows of pits in deep radial sulci. First row near the girder often with comparatively large pits corresponding to the inner row in sulci on upper lamella. (Pl. 10, Fig. 6). Inner margin bent down forming a list, serving as integument attachment.

Genal spine resembling *T. seticornis* and *T. cerioides* with the same section. Terrace lines found.

Marginal rim well developed. Small points or pits found on the surface of test. (Pl. 11, Fig. 12). Marginal suture well defined in this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A67

Fig. 25. *Tretaspis kiæri* n. sp. × 3,3. The same series of sections. Two specimens lying close together. The lower shows the structure of the fringe. *u. l.* = upper lamella, *l. l.* = lower lamella. Distances between the sections: 0,09, 0,09, 0,09 mm.

specimen. Upper rim overhanging the lower, which is separated by a distinct line. In sections the suture appears as a distinct line (Pl. 14, Fig. 3); no thinning of shell is present. Marginal suture follows the marginal band posterior to the genal spines which are crossed at the base. Posterior margin of fringe is crossed obliquely on the vertical posterior band.

Thorax only known in inferior fragments.

Pygidium known from internal casts. Posterior outline semi-circular. Rachis rather narrow. On the lower surface of shell appendifers are visible as darker spots. (Pl. 10, Fig. 4). Fig. 38 shows the arrangement of the 10 pairs of spots of which 3 pairs lie on the nearly vertical posterior band. The structure is discussed p. 93. Pleurae faint on the internal casts.

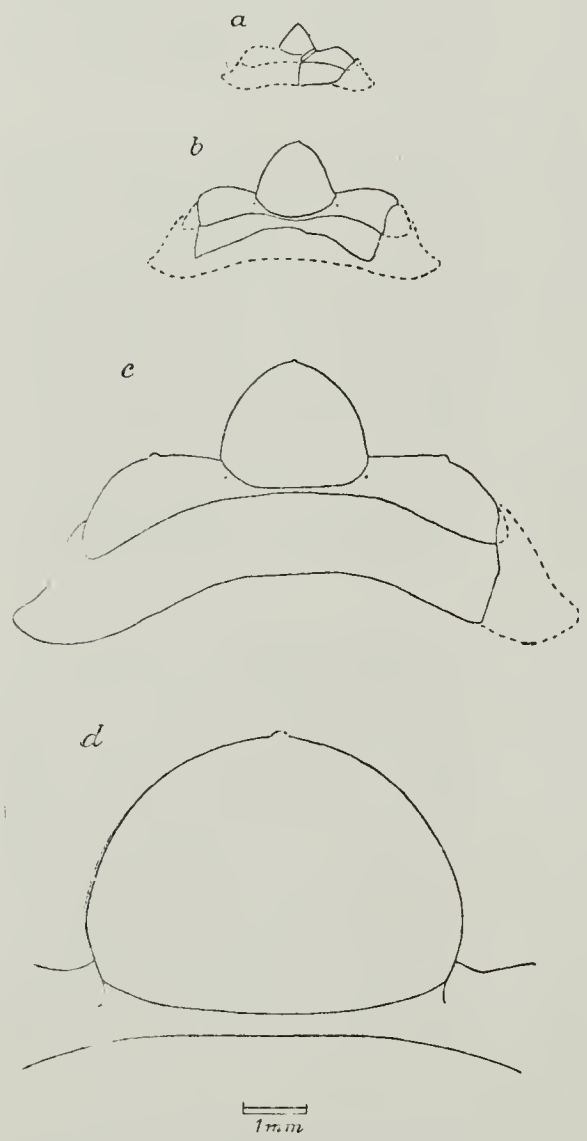


Fig. 26. *Tretaspis kiæri* n. sp. × 5. Development of Glabella. Anterior view of cephalon. *a* = H 354, *b* = H 355, *c* = H 222, *d* = H 353. Lower Trinucleus limestone Frognø, Ringerike. (Kiær. coll. Pal. Mus. Oslo).

Larval stages. Of the numerous specimens examined only a few Meraspid stages are found. One cephalon of 1,0 mm in length present. (Fig. 26 a). Glabella carinate, egg-shaped, without pseudo-frontal lobe. Median and lateral tubercles prominent. Glabellar furrows faint, transverse, resembling those in *Reedolithus carinatus*. Fringe steep, broad. Genal prolongation only indicated. 4 rows of pits in front. Only one row on outer band, lower lamella. It is of interest to note the rather steep outer band resting on a "pseudogirder" anterior as in early stages of *T. seticornis* (p. 62), and *Cryptolithus dicors* (p. 42). The stage corresponds in size and morphological characters to St. II of *T. seticornis*.

One specimen (H 356) of cephalon length = 3 mm has a fully developed fringe.

During the Meraspid and later stages a successive transmission of glabella takes place. Fig. 26 shows the shape of the glabella in anterior view from St. II up to adult. The carinate glabella gradually grows more arched. No rapid change in the characters are found in *Reedolithus carinatus*.

Dimensions. Average length of cephalon in adults = 8 mm, breadth 17 mm. Average length of pygidium about 4,5 mm, breadth 13 mm.

Occurrence. Abundant in a calcareous lens in the lower Trinucleus-limestone at Frognø, Ringerike. One specimen probably belonging to the species was found at Norderhov, Ringerike.

Affinities. The species is allied to *T. cerioides*, *T. granulata* and *T. latilimbus*. It differs from the first only in the number of pits which is seen in the graphs, Fig. 21. The other characters are very similar, suggesting a close relationship. *T. granulata* (from the original of WAHLENBERG and the descriptions by REED 1906—07) shows faintly reticulated or smooth surface of glabella and cheek lobes. Arrangement of pits is the same in the anterior portion of fringe, but the long genal prolongations have about 13—14 pits along the posterior margin (Cp. Fig. 31). *T. latilimbus* has a very narrow brim of fringe. Radial sulci with 2 rows of pits and outer band on lower lamella carries one row.

Tretaspis seticornis. (HIS.)

Pl. 7, 8, 12, Pl. 11, Fig. 1—7, Pl. 13, Fig. 1, 2, 5—7, Pl. 14, Fig. 4—5.

1840 *Asaphus seticornis*, HISINGER, p. 3, Pl. 37, Fig. 2.
— — *cyllarus*, — — — Fig. 3.
1843 *Trinucleus seticornis*, PORTLOCK, p. 263, Pl. 1 B, Fig. 8?
1845 —„— LOVÉN, p. 107, Pl. 2, Fig. 2.
1852 — *bucklandi*, BARRANDE, p. 621, Pl. 30, Fig. 14—16.
1851—54 — *seticornis*, ANGELIN, p, 84, Pl. 40, Fig. 10.
— — *affinis*, — — — 20, 21 e?
1884 — *seticornis*, TÖRNQUIST, p. 84.
1894 — — J. G. ANDERSSON, p. 532, Fig. 1—5.
1894 — — F. S. SCHMIDT, p. 71, Pl. 5, Fig. 19—22.
1906 — *cerioides*, OLIN, p. 67, Pl. 4, Fig. 2.
1906—07 — *seticornis*, FEARNSIDES, ELLES, SMITH, p. 122, Pl. 8 Fig. 7—8.

Distinguishing characters. "Glabella bulbous, rather broad. Surface of shell smooth or faintly reticulated. Eye tubercles present. Fringe narrow with large pits. Upper lamella with two pits in deep radial sulci anteriorly. Cheek roll with usually two rows of pits, radially arranged. On lower lamella one row of pits on outer band anteriorly. Girder prominent."

The classical occurrence of this form is in the black Trinucleus-shales in Dalarna, Sweden. The white shells are easy distinguishable in the black shales. The fossils are pressed and therefore many illustrations of this form give incorrect information of the shape.

The Norwegian specimens of this species replace in a brilliant way the Swedish ones. The specimens from the transition beds in Trinucleus-shale and limestone from Norway are often beautifully plastically preserved. The correct position and shape of the fringe may be studied.

General Description. Some complete specimens have been found. The thorax and pygidium are often bent up posteriorly (Fig. 47). This is probably due to destruction of muscles.

Fig. 27 gives a restored illustration of the species.

Cephalon of semicircular outline with short genal prolongations. Glabella prominent. Broad pseudo-frontal lobe. Surface smooth, faintly reti-

culated (Pl. 11, Fig. 5, 7). The smooth specimens usually seem to have the narrowest fringe. Internal surface with small granulae. Internal casts of glabella show a distinct median tubercle with two diverging lists running anteriorly having a pair of small pits in the lateral portion. (Pl. 11. Fig. 3, and text Fig. 40 p. 96). Median tubercle visible on the upper surface as a rather flat pustule (this is described in a special chapter p. 84).

Axial furrows deep with antennuary pits. Cheek lobes smooth or faintly reticulated. Lateral eye tubercles little elevated. Genal cecae often visible, usually bi-branched.

Fringe very narrow. Whether the narrowness is primitive or not cannot be decided. Upper lamella with steep cheek roll and narrow brim. Brim with about 32 short radial sulci with 2 rows of pits. Anteriorly the short sulci appear as large round pits. Laterally the outer row of pits is divided forming a new row. On the cheek roll usually 2 rows of radially arranged pits are present.

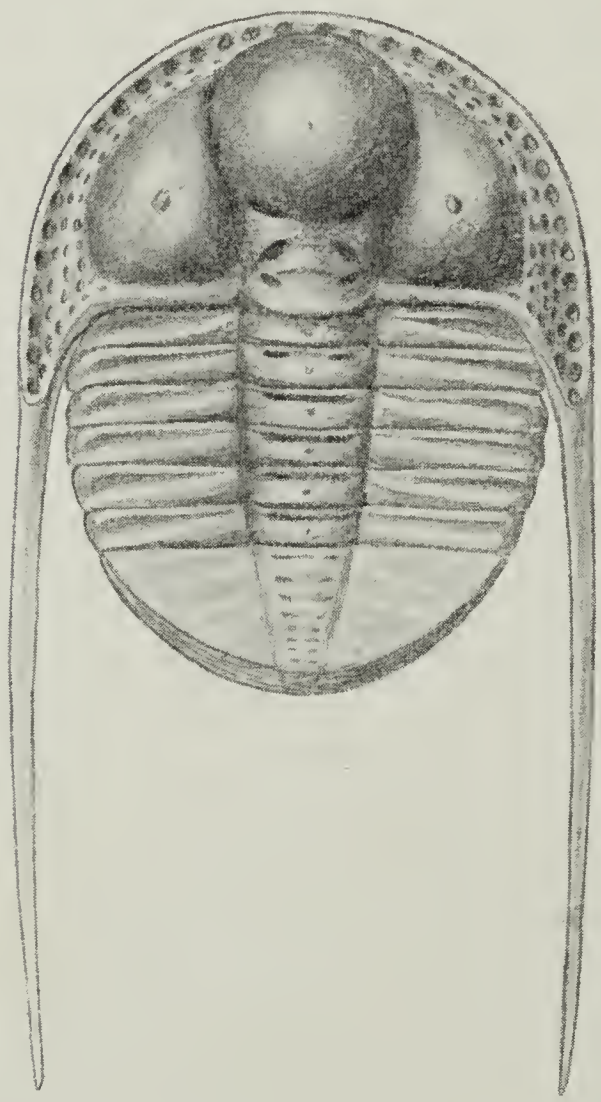


Fig. 27. *Tretaspis seticornis* (His.) Restored specimen. × 3.

Lower lamella lost in half the Norwegian specimens examined. Marginal suture distinct on the vertical marginal band. Small pits or points present on the shell surface (cfr. p. 100).

Lower lamella with a very prominent girder. Pl. 11, Fig. 2 gives an idea of the two lamella in correct position. Lateral portion of outer band tapering at an angle of about 45° against the margin. Outer band carries a single row of pits anteriorly, laterally a new row is developed. Inner band with 2—3 rows in radial sulci. Upper portion with a concentric list for integument attachment. The lamella first bends down then turns and bends upwards forming a list lying close to the other.

Thorax known from several specimens. Only one enrolled specimen. The position of thorax to cephalon may be studied on the complete specimen Fig. 47, p. 106. Thorax beautifully preserved in the specimen from the Trinucleus-shale, Dalarne, Sweden (Pl. 8). On the rachis a faint median ridge or tubercle is indicated on each segment. Articulating furrow narrow, containing deep lateral appendifers.

Pleural furrow broad and shallow laterally. Posterior band with the oblique ridge is prominent near rachis. Lateral limits of pleurae conform with the general outline of thorax.

Pygidium with evenly curved posterior outline. Rachis rather broad. Usually 7 appendifers anterior to the posterior band. Pleurae only slightly marked. Posterior band with terrace lines.

Dimensions. The average length of cephalon 7—7,5 mm, breadth 14 mm. Length of pygidium 3,5—4, breadth 10 mm. The relations of the dimensions are suggested in the restored specimen Fig. 27.

Remarks. From the Swedish localities the size of the specimens found varies to a great extent. All stages of growth are present. In most of the Norwegian localities almost only adult specimens are found. About half the number of individuals have lost the lower lamella of fringe. In Asker a single locality is known which contains young stages of *Tretaspis seticornis*. Some specimens (H 188) from the upper Trinucleus limestone at Frognø, Ringerike, show the branches of bryozoe covering the upper and underside of the fringe anteriorly. The thin branches occur almost only on the ridges between the pits. It cannot be decided whether the phenomenon represents a symbiose or the bryozoe has come on the shell after the death of the trilobite.

Occurrence. In Norway the species occurs in the Trinucleus shales and limestones in the Oslo field. At Oslo the black Trinucleus shale is very poor in fossils. Only scanty fragments of *T. seticornis* are found. In the Trinucleus limestone a single specimen seems to belong to this species. It is found together with *T. latilimbus*.

At Ringerike the species is abundant in the upper part of the Trinucleus shale and lower part of the limestone. The two horizons chiefly lie within an extent of 10 m. The specimens from the two horizons are illustrated in the graphs of variation in Fig. 33, p. 79. The differences between the two graphs are very small, but it may be mentioned that the younger specimens have usually more pits in front (II, III) than the older ones. In the middle of the shale some specimens with rather many pits are found. Below the shale, just in the upper part of the lower Trinucleus-limestone, a specimen was found having indices: I 7, II 4, III 4. It occurred only 1,5 m above the bed with *Tretaspis kiæri*.

In the Langesund district the species is found in the black metamorphic Trinucleus shale at Brevik. The specimens are preserved in pyrrhotite. At Venstøb the species occurs in grey shale.

In Sweden the species occurs in the typical black Trinucleus shale in Dalarne and Østergøtland. It is also found in Kinnekulle, Vestergøtland, according to Linnarsson (1869, p. 79). In Scania the form described by Olin as *T. cerioides* probably belongs to this species.

Andersson (1894) gives a very good description of the species from Øland. The fringe in the specimens described by him shows rather many pits. A third row of pits is indicated on the cheek roll. Variation of pits is depicted in the graphs Fig. 33, 34. The species from Dalarne and

Østergøtland show an indication of a smaller number of pits than the Norwegian species. The species is found in Estland in the Lyckholmer beds. From Bornholm Ravn (1899) quotes two species of *Tretaspis* in the Trinucleus shale. Examining the material in Copenhagen I found one specimen with indices I 8, II 4,5, which is probably *T. seticornis*. From Bohemia Barrande (see above) has described forms belonging to this species. He suggested that they were young stages of *T. granulata* var. *bucklandi*, but the character of pits agrees with *T. seticornis*. Some specimens from Grand-Manil, Belgium, in the Riksmuseum, Stockholm, probably belong to this species.

In the British isles *T. seticornis* occurs in Tyrone, Ireland, and probably in Girvan and in Applethwaite, Norber Brow, and Cynwood (Reed 1912, p. 392).

The species is spread all over the north of Europe.

Affinities. The species is nearest related to *T. latilimbus* which differs by its broader fringe carrying more rows of pits and the shallow radial sulci on the brim. The younger *T. latilimbus* is possibly related to the older *T. seticornis* (cp. p. 83). *T. cerioides* differs from the present species by the broader anterior fringe and the strong reticulation.

The ontogeny of *Tretaspis seticornis* (His).

In the typical black Trinucleus shale of Dalarne and Västergötland, Sweden, *Tretaspis seticornis* is very common. Beside the adult specimens a number of different younger stages are found. Törnquist mentions in his paper on the trilobites from Dalarne (1884, p. 85) that smaller stages of *T. seticornis* were found, the smallest having 4 thoracic segments. The small stages had reticulated glabella with indistinct glabellar furrows. No genal prolongation in the smallest stages, but obtained during later stages.

In the Geol. Inst. in Lund I had an opportunity of examining the collections of Törnquist. His collections and some made by Dr. Isberg gave a valuable material for describing the small stages. Interesting material was kindly lent to me for description from the Geol. Inst. in Lund and the Riksmuseum in Stockholm.

Preservation. Only a few pieces of the shale contain the well preserved small stages. The preservation in shale gives little idea of the shape of the fossil. The arched portions are pressed and in some cases crushed. The surface however, shows very fine details. The specimens from Dalarne have the shell preserved in a white matrix which is well separated from the black shale.

The white colour is not found in the specimens from Østergøtland.

In the ontogeny of trilobites the protaspis or Protaspid period (Cobbold, Raw) (Raw 1925, p. 226) is characterised by a fusion of the

cephalon and the transitory pygidium. The Meraspid period is characterised by the successive appearance of each of the thoracic segments. When the complete number of thoracic segments is attained, the Holaspid period begins. RAW (1925 p. 225), STUBBLEFIELD (1926 p. 351) adopted the term Degree, used by BARRANDE for the different stages in the Meraspid period. The term stage or abbreviated St. is used in this paper. STUBBLEFIELD says: "The last thoracic segments to appear in *S. [Shumardia] pusilla* is the sixth, so the final degree of the Meraspid period will be Degree 6". It seems more practicable to reckon the stage as the first Holaspid stage. Otherwise the lower limits of the Holaspid period would be difficult to establish.

Complete specimens of the young stages are rare in the black Trinucleus shale. Pl. 7, 8 show that it has been possible to find complete specimens of St. I, III, IV, V. St. O was found with the pygidium lying just beside. Two enrolled specimens of St. II give little idea of the thorax and pygidium. Several complete specimens from the Holaspid period are known.

The chief part of the material described consists of single cephalae and pygideae.

The Meraspid stages can be determined in two ways: (1) by measurements of size and (2) by examination of the morphological characters.

Measurements of size.

Within the arthropoda growth takes place during several moultings. The chitinous shell is periodically shed. The addition of length during growth is obtained almost only just after the moulting when the shell is soft. The trilobite shells found always represent the hardened chitinous shells. It is a question whether the shells found belonged to dead animals, or were empty sloughs from the moultings. The individuals with

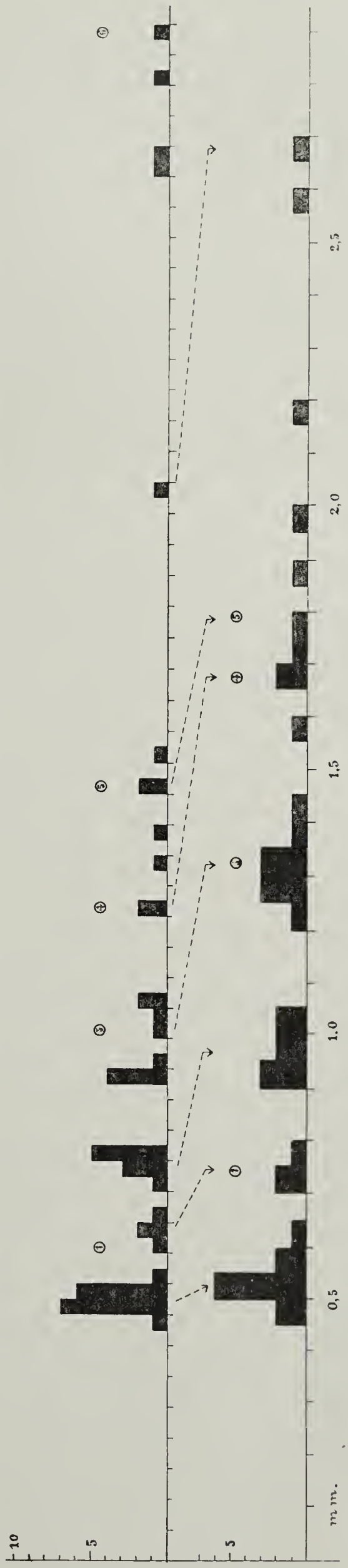


Fig. 28. Measurements of the youngest stages of *Tretaspis seticornis* (His) from Dalarne. Explanation of the graphs on p. 60.

soft shells at the period just after the moulting are not preserved. This period represents the period of growth of size. If the moulting of Trilobites takes place at certain fixed stages, and the stages are connected with a definite size of the animal, certain groups of size should be much more common than others. Within the recent crustacea distinct groups of size have been separated, representing the individuals with hardened chitinous shell. GRAN (1902) and several later authors have e. g. distinguished the different copepoded stages of the copepode *Calanus finmarchicus* GUN. by definite groups of size.

Measurements have been made of the small specimens of *Tretaspis seticornis* from Sweden. The measurements are shown in the graphs Fig. 28. In the graphs the absciss gives the size. The ordinate the number of specimens measured. Both graphs are based on the same material. In the lower graph the absciss represents the median length of cephalon, in the upper the length of the axial furrow from the fringe to the posterior margin of cephalon is measured. The specimens in the lower graph have been directly measured in a binocular microscope by means of a scale showing 0,05 mm. The measurements of the upper graph were made with a measuring-ocular. The scale in the lower graph also applies to the upper one, although the colums in the graph are based on a relative scale.

As the measurements of the axial furrow are smaller than those of the length of the cephalon the correspondence of the different groups of size is indicated by a →. The columns with complete specimens are marked by a ring above containing the stage number.

The number of specimens examined is rather small. The pressures of the well arched cephalons in the shales give errors in the length. The axial furrow has been chosen (upper graph) on account of its straight, only slightly arched course. The two graphs clearly show an uneven distribution of the size of the young larvae. Several definite groups of size are distinguishable. As described below the different groups of size well agree with the stages, separated by distinct morphological characters. The 3—4 earliest stages are well marked.

No considerations of the variation of size within the different stages can be made on the basis of the rather scanty material.

The graphs show, what has been generally assumed: The growth of trilobites takes place through a number of moultings. The graphs also show that the moulting in the Meraspid period of *Tretaspis*, and probably other trilobites, is closely connected with distinct sizes of the body.

Description of the Larval Stages.

No specimens from the Protaspid period are found. This is probably due to the very soft shell of the trilobite in the very early stage. Small larval stages of ostracoda were found which were probably smaller than the later Protaspid stages. The different Meraspid stages are described in the following.

Stage O. (Degree O).

Corresponding to the first group of size in Fig. 28 a number of specimens occur which show the same general characters. Pl. 7, Fig. 1—4 shows specimens of this stage. Of the 15 measured specimens only a few were well preserved. The shell, as mentioned, seems to have been very thin and soft in this stage. Similar conditions were found in *Reedolithus* (p. 34). Cephalon broad. Glabella strongly pressed in all specimens, median portion probably carinate. Glabella narrow, broadening anteriorly. Indications of segmentation of posterior portion, (Pl. 7, Fig. 2, 3) might have been caused by pressure. Large median tubercle present (Pl. 7, Fig. 3). Occipital ring distinct. Laterally to posterior part of glabella distinct triangular fields. Lateral part consisting of a broad shallow furrow or depressed field, narrowing anterio-medially forming distinct axial furrows. Inner part of the triangular fields occupied by faintly elevated, lunar-shaped alae. Posterior part crossing the occipital segment like faint ridge (Pl. 7, Fig. 2—3). Inner part of alæ well bounded from the central portion of glabella.

Cheek lobes arched. The lateral division by furrows seen in Pl. 7, Fig. 2 is probably due to bad preservation. Short, transverse eye-lists with faintly developed lateral eye-tubercles.

Occipital segment broad. Occipital furrow distinct laterally, nearly absent posterior to the triangular fields.

Fringe flat, narrow. Greatest width posterio-laterally. Distinct pits not traced with certainty on the upper lamella. On Pl. 7, Fig. 2 small indication visible anterior to glabella. The visible portion of fringe corresponds to the upper marginal brim which is very broad in the youngest stages.

Lower lamella found in one specimen (Pl. 7, Fig. 4). Outline trapezoid. A list corresponding to the lower marginal rim forming the chief width of the lamella. The list continues in the genal spines. Within the list a narrow furrow with some very small, but distinct pits. The pits only visible anteriorly. Within the furrow a narrow list, probably the attachment of integument found in later stages. Genal spines, preserved in one specimen (Pl. 7, Fig. 1), are of considerable length. Pl. 7, Fig. 3 illustrates a specimen having the marginal suture preserved. The fringe laterally to the marginal suture is well marked on the original. The photo does not show the brown coloured lateral portion very well. It is of interest to recognize the course of the marginal suture which is near the margin in front and across the fringe posteriorly.

A pygidium was found together with the cephalon in one case (Pl. 7, Fig. 2). Two segments and traces of rachis are indicated on the thin-shelled specimen.

Stage I. (Degree I).

This stage also well defined in the graphs Fig. 28, p. 59.

Pl. 7, Fig. 8 shows a complete specimen with the single thoracic segment and pygidium a little out of position. Cephalon broad. Glabella a little broader than in the former stage, probably carinate. Median tubercle present. Alae distinct. Alar furrow narrower than in St. O. Cheek lobes with reticulated surface. Eye lists oblique, lateral eye tubercles only indicated.

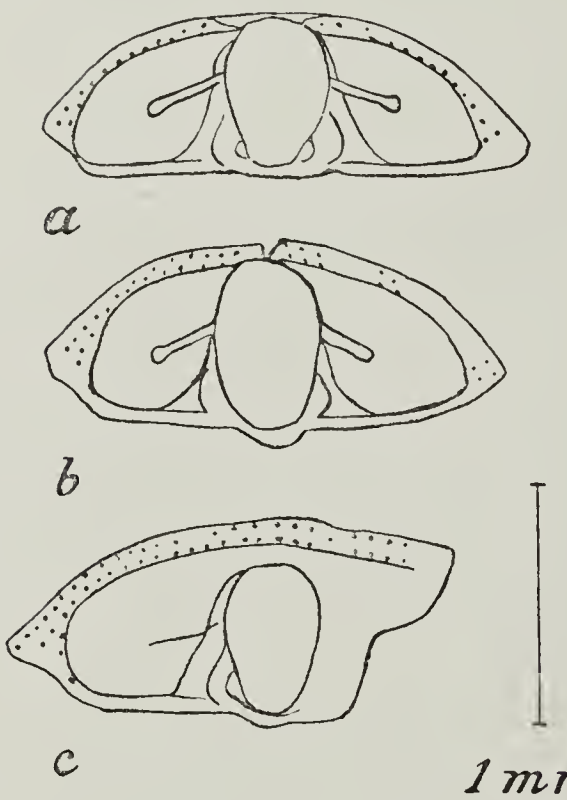


Fig. 29. *Tretaspis seticornis* (His.) × 19. Variation of Meraspid stage I. Trinucleusshale. *a* — *b* from Dalarne *c* from Östergötland. *a*, *b* = Ar. 2287, Ar. 2294. Riksmus. Stockholm. *c* = 21 *b*. Geol. Inst. Lund.

Fringe well preserved in the present specimens, a little broader than in St. O. Fig. 29 illustrates the arrangement of pits on the fringe. On the two specimens from Dalarne two rows of pits radially arranged are found anteriorly. Laterally the radial arrangement is lost, and the two rows are reduced to one. No sulci visible. The specimens from Östergötland have two distinct rows of pits all round the fringe. The differences certainly represent individual variations, comparable with those found in the adults. (Cp. Fig. 33, 34, p. 79, 81). Also the adult specimens from Östergötland indicate a greater number of pits posterio-laterally than those from Dalarne (Fig. 34, p. 81 and Fig. 1, p. 10).

Pl. 7, Fig. 5 illustrates the anterior portion of a lower lamella from Östergötland. The number and arrangement of pits indicates St. I. The broad outer list with arched posterior surface. The steep inner portion of fringe with two rows of pits and an inner list for integument attachment. Between the two rows only a very faint ridge indicated. This ridge in later stages becomes the girder. In St. O, and I the broad lower marginal rim is developed as a "pseudogirder".

Lateral portion of lower lamella shown on a specimen from Dalarne Pl. 7, Fig. 6. Arrangement of pits quite corresponds to the upper lamella. Marginal rim very broad and distinct. Genal spine well preserved. Length and direction fairly well corresponding to the adult specimens. Width considerably greater.

Length of pygidium about 2:3 of cephalon. Rachis little marked from the triangular elevated portion on the pleura. The elevated median portion corresponds in outline to glabella with triangular fields.

Stage II. (Degree II).

Stage II well defined in size and morphological characters. 8 specimens present: Two complete enrolled individuals (Pl. 7, Fig. 12). Pygidium and the two segments of thorax preserved on the lower side of cephalon, not as in *Agnostus* where cephalon and pygidium are of equal length.

Some beautifully preserved specimens occur (Pl. 7, Fig. 9,10 and text Fig. 36, p. 86). Surface of shell shows the minutest details.

Glabella strongly arched, reticulated in the median portion. The steep sides smooth. Distinct, large median tubercle. The structure of the tubercle described in details p. 84. Glabellar furrows not very distinct in the pressed specimens. Traces of posterior pair present. Occipital ring distinct. The lateral lobes or alae well separated from central portion of glabella. Axial or alar furrows have become narrower and with a more longitudinal course. Axial furrows diverging slightly posteriorly. Antennuary pits indicated.

Cheek lobes arched with reticulated surface on the median portion, and a smooth band against the fringe. Eye list distinct, rather broad near the axial furrow. Lateral eye tubercle not as well defined as in the later stages. Occipital segment broad.

Fringe has in this stage nearly obtained the general characters of the adult. Anteriorly two double rows of pits. Pits in each of the double rows radially arranged. The marginal double row is not radially arranged to the inner double row. In stage I two rows of pits with little radial arrangement were found. This makes it highly probable that the two single rows in St. I have developed by division of pits into two double rows in St. II.

Upper lamella with about 35 pits in outer row. The two marginal ones with pits in radial sulci which become absent laterally.

The two inner rows, in some cases, Pl. 7, Fig. 9, lie in radial sulci. In Pl. 7, Fig. 10, the rows are separated by a concentric ridge. The latter represents the complete separation of the rows of pits. Laterally in the occipital furrow one single pit is found separated from the other. It certainly represents a hollow pillar and thus the inner limit of fringe. Along the posterior margin 5—6 pits are found.

Lower lamella visible on Pl. 7, Fig. 11. The double nature of the two rows of pits not very distinct. The broad marginal rim forming a "pseudo-girder". In this stage the girder is developed within the first row of pits. Laterally 5—6 pits are faintly indicated. Indications of radial sulci on inner band anterior.

Thorax and pygidium not known in well preserved specimens.

Stage III. (Degree III).

The size group on Fig. 28, p. 59 is well marked, but does not show a distinct maximum in the middle in the upper graph. One complete specimen visible on Pl. 8, Fig. 1.

Glabella well arched, a little broader than in St. II. Reticulated surface with median tubercle, Two posterior pairs of glabella furrows indicated. Lateral lobes (alae) narrow, well marked from central portion of glabella. Axial furrows nearly longitudinal.

Cheek lobes reticulate with distinct lateral eye tubercles of size of median tubercle.

Fringe (Pl. 7, Fig. 13) not very different to St. II. In the lateral portion of some specimens the marginal row of pits is divided. At the genal angles some pits are added forming a number along the posterior margin of about 7. Anteriorly some individuals have only one row of pits on the cheek roll where two rows were found in St. II. This is due to individual variation. The adult in some cases (Fig. 34, p. 81) shows only one row of pits on the cheek roll. Lower lamella unknown at this stage.

Thorax badly preserved. Rachis narrow. Pleural furrows distinct.

Pygidium with two well defined segments. Rachis not well separated from the elevated median portion of pleura.

Stage IV. (Degree IV).

The size group in Fig. 28 not well defined. Some complete specimens are found (Pl. 8, Fig. 2).

Glabella a little broader than in the former stage. Pseudo-frontal lobe indicated. Surface reticulated. Median tubercle present. 3 pairs of glabellar furrows, of which the first pair is only indicated and the posterior more distinct in a transverse position. Lateral lobes (alae) narrow, reduced anteriorly. Distinct longitudinal axial furrows. Cheek lobes reticulated, with lateral eye tubercles larger than the median tubercle.

Fringe nearly as in St. III. Genal prolongations only indicated. Pl. 7, Fig. 15, a specimen from Østergøtland, has a large number of pits. Outer and inner row of pits are divided laterally. 9 pits along the posterior margin.

Lower lamella with distinct girder (Pl. 7, Fig. 14). Thorax with distinct appendifers and pleural furrows. Pygidium hard to separate from thorax on account of two well-defined segments in the anterior portion.

Stage V. (Degree V).

A certain group of size cannot be traced (Fig. 28, p. 59). Pl. 8, Fig. 3 shows a complete specimen. Glabella with pseudo-frontal lobe. Distinct glabellar furrows. Lateral lobes not well separated from central portion of glabella. Axial furrows slightly converging posteriorly.

Cheek lobes and fringe as in the former stage. Only a little more developed genal prolongations.

Holaspid stages.

The smallest complete specimen from the Holaspid period (Pl. 8, Fig. 4) has a size double that of the depicted specimen of St. V. Glabella with pseudo-frontal lobe, but not as prominent as in adult specimens. Glabellar furrows rather transverse. Reticulation of glabella and cheek lobes disappear during the Holaspid period. Small genal prolongations of fringe. Pygidium with 8 pairs of appendifers.

Change of the different morphological characters during the ontogenetic development.

Outline of body nearly hexagonal in the earliest stages. During the growth the body is prolonged by the addition of thoracic segments. Outline of cephalon changes from broad trapetzoid to semicircular.

Shell very thin in earliest stages. The reticulated surface found in the Meraspid stages is reduced during the Holaspid period.

Before regarding the development of glabella the course of the axial furrows, representing the lateral limits of glabella, will be discussed.

The earliest stages of *Cryptolithus* (Barrande, 1852, Beecher 1895), *Trinucleus* (p. 28) and *Reedolithus* (p. 34) all show the same general characters. The narrow carinate glabella, or median portion of glabella, has posterio-laterally well marked, triangular fields consisting of a faintly elevated semilunarly shaped inner portion, and a broad shallow furrow laterally. The inner portion has been compared (Beecher, 1895) with similar shapes found in *Harpes* termed alae or alar fields. The oblique lateral furrows would correspond to the alar furrows.

During the development of the alæ in *Tretaspis* (and also in *Trinucleus*, *Reedolithus* and *Cryptolithus*) the broad, oblique alar furrow becomes narrower and gets more and more a longitudinal direction. At last it is transferred into the axial furrow in the later stages. The rather flat alae, well-marked in the earliest stages, becomes, during the ontogeny, narrower and more elevated in the median portion. At the later stages they are not well marked from the central portion of glabella, the alæ are quite transferred to the lateral lobes of glabella.

Reed (1914, p. 350) has shown that the lateral lobes of Trinucleidae belong to the glabella (cp. p. 34).

From this we may conclude that the alae in the young stages of Trinucleidae belong to the glabella, and the axial furrows strongly diverge from the anterior portion of glabella posteriorly. On account of the close resemblance of the alae in *Harpes* and young Trinucleidae we must assume that the alæ of Harpedidae belong to the glabella.

In *Tretaspis seticornis* the broad posterior portion of the axial furrow may be compared with the outer of the two sub-crescentic alæ.

The median portion of glabella grows broader during development. In the earliest stages no pseudo-frontal lobe is marked. The glabellar furrows cannot be traced until St. III. The furrows have a transverse position.

Median tubercle is very prominent in the early Meraspid stages. The ontogeny is described on p. 87.

Cheek lobes become narrower in the later stages.

Lateral eye tubercle only slightly developed in the earliest stages. St. II has not a well defined eye tubercle. St. III and IV have distinct tubercles. The ontogeny discussed p. 90.

Eye-lists hard to distinguish in St. O. They seem to be transverse and short. In the later stages the lists become more distinct, longer and rather prominent near the axial furrow. The lateral eye tubercles pass against the genal angles, a short distance.

Fringe. The shape of the fringe is changed during the increase in the width of the fringe. The genal prolongations are not marked in the earlier Meraspid stages, they are developed from about St. IV. Upper lamella having only traces of pits within the broad rim in St. O. The occurrence of pits on the lower fringe indicates a more or less complete row of pits. St. I has 1—2 rows developed. Radial arrangement of pits only slightly emphasized. St. II having two double rows of pits. Distinct radial arrangement within each of the double rows. Pits usually in radial sulci. The two inner rows in the same cases quite separated by a concave list. The close connection in radial arrangement, and radial sulci of the first and second, third and fourth row of pits makes it very probable that the 4 rows have developed by division of each of the two rows in St. I.

The development of new rows of pits not only takes place at the margin, as has been generally assumed, but is also found at the inner portion of the fringe. A fact which is noticed in several of the above described species of *Reedolithus*, *Cryptolithus* and *Tretaspis*. Besides the two double rows in St. II, some few pits are intercalated posterio-laterally. The later stages are not very different to St. II. Some more pits are developed along the posterior margin. The development of new rows of pits through division of pits in radial sulci is noticed.

Lower lamella corresponds to the upper in the arrangement of pits.

In the earliest stages, St. O—II, the broad lower marginal rim is developed as a "pseudo-girder". No traces of the real girder are found until St. II where it is developed besides the "pseudo-girder". It is found within the marginal row of pits. In the later stages it is well marked.

Genal spines long and broad in the earliest Meraspid stages. Well developed from St. O. They grow narrower in the later stages. Marginal suture found in all stages. In St. O the marginal suture is found crossing the dorsal portion of upper rim. In the later stages it is quite marginal (cfr. p. 92).

Thorax. Some changes in the different segments added during the Meraspid period. The earliest segments show pleurae with fulcrum and slightly deflated pleura. The latest segments show short nearly vertical lateral pleurae.

Pygidium with very faintly marked rachis in the earliest stages. It is connected with the elevated, triangular inner portions of pleurae. The shape of the elevated portions might be compared with the triangular outline of glabella. The 1—2 anterior segments are very distinct in the Meraspid stages. In the Holaspid period the number of appendifers seems to have increased from 6 to 7.

Tretaspis latilimbus (Linrs.).

Pl. 11, Fig. 8—11.

1869 *Trinucleus latilimbus* Linnarsson Pl. 2, Fig. 46—48.

Distinguishing characters. "Glabella narrow, with semispheric pseudofrontal lobe. Surface of shell smooth. Fringe steep, broad anteriorly. Brim faintly developed with very shallow radial sulci containing two and seldom 3 rows of pits. Cheek-roll with 3—5 rows. Lower lamella with narrow outer band, containing one, seldom two rows of pits. Narrow girder with 4—6 rows in radial sulci on inner band".

The species was described by Linnarsson from the Trinucleus shales at Västergötland, Sweden. It is very common in the layers. Recently Kand. Junge in Uppsala made new valuable collections which he kindly showed to me. He will perhaps give a new account of the species from Västergötland.

The Norwegian species, specially that found in the upper Trinucleus limestone agree with the Swedish form. The form from the upper Chasmops zone shows slight differences.

The description is based on the Norwegian specimens; the type specimen has been chosen in the material from Linnarsson or from new collections in the same locality.

General description. Glabella rather narrow. Strong pseudofrontal lobe with median tubercle. Surface of shell usually smooth in adult specimens (H 265). Younger stages (H 269) have reticulated surface. Three pairs of glabellar furrows. First pair very faint, posterior pair rather short. Occipital ring broad without occ. spine. Cheek lobes well arched with distinct lateral eye-tubercles. Axial furrows distinct having antennuary pits in front.

Fringe very steep and broad. Angle of declination about 70—80°. Brim nearly absent. Cheek-roll occupies almost the complete breadth of the fringe. Upper lamella with the two outermost rows of pits in very shallow radial sulci. This is not indicated on Linnarsson's figure (1869).

On some specimens the outer row is divided into two rows lying close together. Number of pits in the outer row about 38—40. On the cheek-roll 3—5 rows are found radially arranged. Rows probably separated with concentric list. Genal prolongations rather short. Lower lamella with narrow outer band carrying one row of pits. In some few specimens a row is divided into two closely connected rows. The single row continues posteriorly to the genal spine. Girder narrow. Inner band with 4—6 rows of pits in radial sulci. First row often separated from the sulci on account of a different radial arrangement. Pits often beautifully preserved. Pl. 11, Fig. 10 shows pits on the genal prolongation.

The small openings of the hollow pillars are visible at the bottom of the pits. Number of pits along the posterior margin about 8—10. Genal spines of the usual *Tretaspis* shape, not as in LINNARSSON's drawing (1869). Variation in number of pits seen on Fig. 33, p. 79.

Thorax depicted on Pl. 11, Fig. 9 seen in ventral view. The enrolled specimens show the long appendifers in the lateral portion of the rather strongly arched rachis. Breadth of rachis about 3:5 of pleurae. In the axial furrows the strong articulating joints are visible. Pleural furrow broad Lateral portion bent vertically. Lower surface of thorax and pygidium shows small granulae similar to those found in the cephalon in *Tretaspis*.

Pygidium with arched pleurae. Rachis with 7 appendifers visible.

Larval stages. A small cephalon measuring 0,9 mm in length has 3 rows of pits anteriorly on the fringe. Upper marginal rim broad. The specimens probably represent the Meraspid stage I. It is quite similar to the stage found in *T. cerioides var. angelini* (p. 49).

A cephalon with = 1,9 mm has a complete number of pits on the fringe.

Dimensions. Average length of cephalon of the specimens from Trinucleus limestone about 6 mm, from upper Chasmops zone 8—9 mm. Breadth difficult to establish, but the proportions seem to be the same as in *T. kiæri* and *T. seticornis*.

Length of pygidium 4 mm, breadth 11 mm in the youngest form.

Remarks. The two forms found in the Trinucleus limestone and the upper Chasmops zone differ to a certain degree. The former is identical with the Swedish form. The latter is larger and has usually a somewhat larger number of pits (Fig. 33). The sulci on brim is also more prominent. Outer band on lower lamella a little broader than the earlier form, sometimes showing two rows of pits. The mentioned differences have been found too small to establish a new variety.

Occurrence. The species is found in the Trinucleus limestones of Lindø near Oslo. Fragments are met with in different localities near Oslo. In the Isotelus layers of N. Langø traces of the species are found. In the upper Chasmops zone just below the conglomerate the species is very common in certain layers near Oslo e. g. at Lindø, N. Langø, Husebergø.

In Ringerike the species is known in two specimens from the transition layers from upper Trinucleus limestone to the Isotelus layers. In a Rhabdoporella limestone of the same age, the species was found at Holmen in Asker by KIÆR (1902, p. 9).

Affinities. Differs in the narrow brim and the greater number of pits from *T. seticornis*. The narrow brim and smooth surface of the specimen separates it from *T. kiæri*. *T. granulata* has a considerably larger number of pits, specially on the genal prolongations.

Tretaspis granulata (WAHLB.)

1818 *Trinucleus granulatus* WAHLENBERG. P. 15. Pl. 2, Fig. 4.
1848 — *Wahlenbergi* ROUAULT p. 82.
1899 — *seticornis* (HIS.) var. *bucklandi* NICHOLSON and ETHERIDGE p. 190 Pl. 13 Fig. 13—20.
1903 — *bucklandi* REED. C. p. 10 Pl. 1, Fig. 10—14.

Distinguishing characters. "Surface of shell smooth or faintly reticulated. Lateral eye-tubercles obsolete. Fringe broad with long genal prolongations. Broad brim with 3 rows of pits in radial sulci. Four rows of pits on the steep cheek-roll. 3 inner rows radially arranged. Lower lamella with two rows on outer band, 6 on inner, lying in radial sulci, especially in the upper portion.

In the Trinucleus shales of Bohemia, the British Isles and Scandinavia some large forms of the genus *Tretaspis* occur. The length of cephalon is about 11—15 mm in the adults. The specimens used for description of this species have been differently, but usually badly preserved. This has given rise to several indistinct or erroneous descriptions and illustrations.

The author has had the opportunity of examining the specimens from Bornholm in the museum of Copenhagen, and the species from Scania and Västergötland in the Geol. Inst. of Lund, the Riksmuseum in Stockholm and the Geol. Inst. of Uppsala.

The arrangement and number of pits were examined. The graphs Fig. 32 show the variation of pits. Some drawings of fringe details have been made. In Uppsala the original specimen of WAHLENBERG was found, an impression of cephalon with upper lamella. The specimen of WAHLENBERG, the lectotype, is rather different from many specimens from Scania, Bornholm, Västergötland and Bohemia, which seem to agree in their morphological characters and are preliminary established as a variety.

The lectotype is closely similar to the large *Tretaspis* from the Drummock group in GIRVAN described and depicted by REED (1903—*b* p. 10, Pl. 1, Fig. 10—14) as *Trinucleus bucklandi*.

General description. Glabella well arched with prominent pseudofrontal lobe as in *T. kiæri*. Surface of specimen smooth or faintly reticulated. Cheek lobes with quite reduced lateral eye-tubercles. The lack of

lateral tubercles is probably of little systematic value. The presence of a lateral eye tubercle is however often hard to establish in badly preserved specimens. Younger species of the variety bucklandi have lateral tubercles which have disappeared in the adult. The same seems to be found in the younger stages of the species from girvan, although the earlier authors reckoned *T. seticornis* as a young stage of the larger *T. granulata*.

Fringe with a broad brim and cheek-roll. Prominent genal prolongations. Upper lamella with deep radial sulci containing 3 pits on the brim. 4 rows of pits radially arranged on the steep, slightly convex cheek-roll. Lower lamella with strong girder. Two rows of pits on outer band. Inner band with strong radial sulci.

Dimensions. Cephalon length usually 12—15 mm, breadth about 26 mm. Dimensions of pygidium indicated on the figures of Reed.

Occurrence. Specimens similar to that described by Wahlenberg are found in the Trinucleus limestone in Västergötland. The form from Ashgillian (Drummock group), Girvan certainly belongs to this species.

Remarks. Rouault proposed the name *T. wahlenbergi* instead of *T. granulata* because the impressions of the pits on the fringe had been explained as granulae. The original name is adopted in this paper.

Affinities. The species show a general resemblance to *T. kiæri* which differs in the reticulated glabella and the smaller genal prolongation which gives a smaller number of pits along the posterior margin. *T. latilimbus* has short genal prolongations, narrow brim with shallow radial sulci, characters different to those of the present species.

Tretaspis granulata (Wahlb.), var. *bucklandi* (Barr.).

1822 ? *Trilobites granulatus* Brongniart p. 36 Pl. 3, Fig. 7.
1828 *Asaphus* — Dalmann p. 66 Pl. 2, Fig. 6.
1845 *Trinucleus* — Lovén p. 109 Pl. 2, Fig. 2.
1851—54 *Trinucleus Wahlenbergi* Angelin p. 64 Pl. 34, Fig. 1.
1852 *Trinucleus bucklandi* Barrande p. 621 Pl. 29, Fig. 10—17.
1906 — Olin p. 66 Pl. 4, Fig. 1.
— *elliptifrons* Olin p. 68 Pl. 4, Fig. 2.

Distinguishing characters. "Differs from *T. granulata* by narrow fringe. Irregular arrangement of pits. Sulci with 2 or 3 rows of pits on the brim. 3 intercalating rows of pits on the cheek-roll. Inner row often divided into 2, even 3 rows of small pits in radial sulci".

Together with *T. granulata* at Västergötland a number of specimens occur which differ to a certain degree from the species described above. The differences are located to the fringe. In the other portions no differences are recognized. In Scania and Bornholm only the variety of *T. granulata* is found.

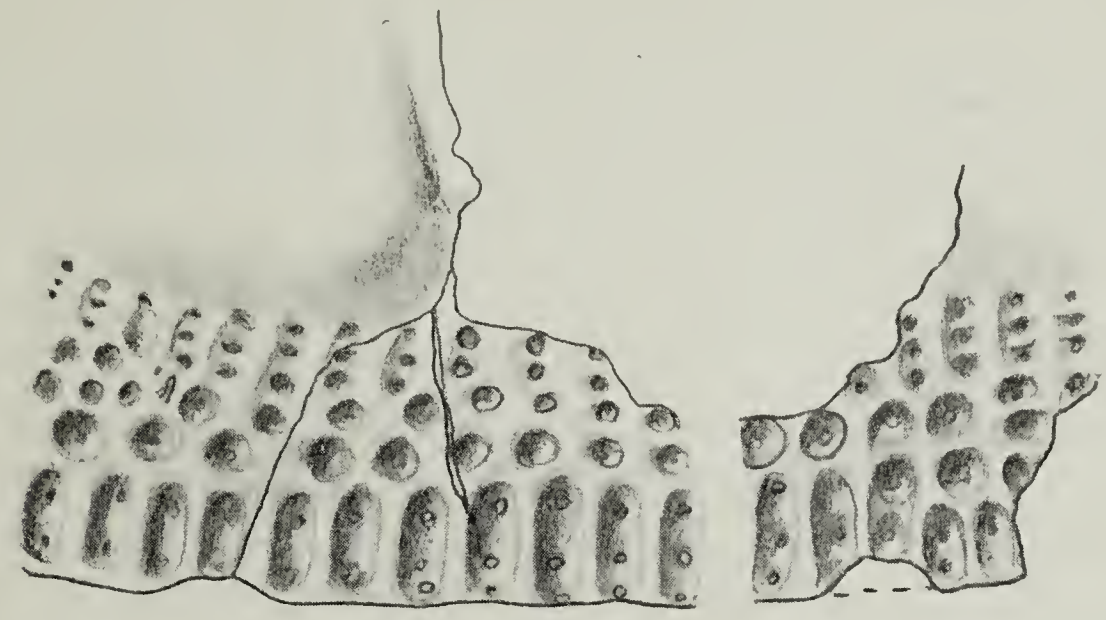


Fig. 30. *Tretaspis granulata* (WAHLB.) var. *bucklandi* (BARR.) × 5. Details of anterior fringe. Trinucleus shale Billingen. Västergötland, Sverige.

General description. Glabella and cheek lobes probably quite similar to those in *T. granulata*. Some specimens from Bornholm show a faintly reticulated shell, but most specimens have a smooth surface of shell.

Fringe rather narrow in front.

Genal prolongations prominent, as in *T. granulata*. Genal prolongations are drawn by ANGELIN (1851—54 Pl. 34, Fig. 1*a*—*c*) and OLIN (1906 Pl. 4, Fig. 7). Brim broad and distinct. In the preservation in shales the brim usually appears flat. Cheek-roll very narrow in front. The variety shows an unusual irregularity in the arrangement of pits. Fig. 30—31 illustrates the arrangement of pits on the upper lamella of two specimens from Billingen, Västergötland. The marginal radial sulci have different lengths. Besides the usual sulci with three pits, shorter ones are found carrying two rows. On the cheek-roll 3 rows of intercalating pits are found. Inner row sometimes divided into 2—3 rows of smaller pits lying in faint radial sulci. (Fig. 3). Laterally the number of rows of pits increases. Along the posterior margin about 13 pits are numbered.

Lower lamella with distinct girder and outer band, laterally the two rows fuse into one. Sulci on the inner band little developed on account of the irregular arrangement of pits.

Thorax and pygidium described by BARRANDE (1852), show resemblance to *T. kiæri*.

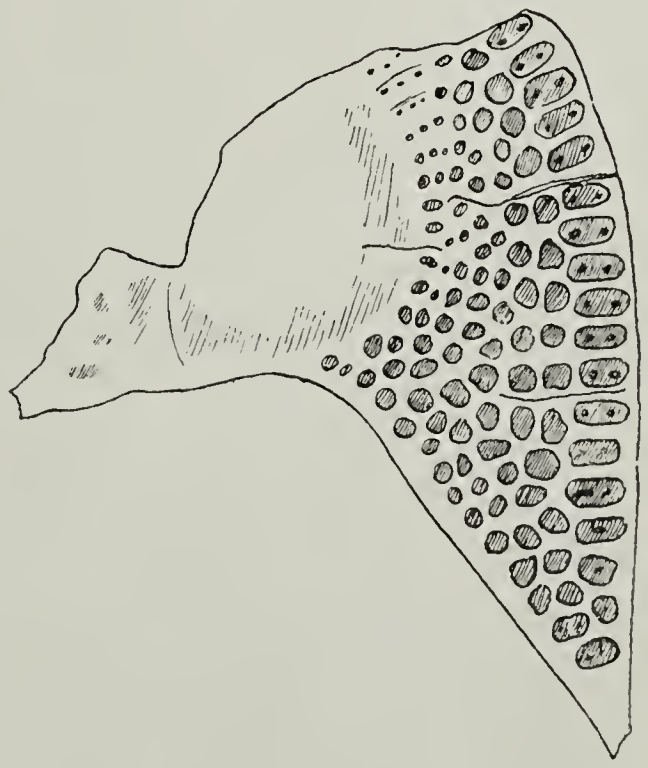


Fig. 31. *Tretaspis granulata* (WAHLB.) var. *bucklandi* (BARR.) × 5. Posteriolateral portion of fringe. Trinucles-shale, Billingen, Västergötland, Sverige.

Dimensions. Length of cephalon about 12—15 mm. Dimensions are difficult to establish on the badly preserved Scandinavian material. The descriptions of the better preserved Bohemian specimens (BARRANDE) give a more correct impression of the proportions.

Remarks. The material examined and the time available for studying the collections in Denmark and Sweden have not been sufficient to decide the limits of variation of the above described morphological characters. It might perhaps be possible to find a transition between the two forms that excludes the present established variety.

The grounds for proposing a new variety are as follows: (1) The different morphological characters are found in a number of specimens. This is depicted in Fig. 32 where the column of II and III with 6 pits represents the variety. (2) In Scania and Bornholm only the variety is found. In Västergötland both forms are mingled. The great breadth of variation indicates a mixture of several forms.

The species described by OLIN (1906 p. 68, Pl. 4, Fig. 2) as *Trinucleus elliptifrons* certainly belongs to the variety of *T. granulata*. I had the opportunity of examining the original specimen which probably has obtained the narrow glabella by pressure.

A Norwegian fragment of fringe measuring 9 mm across the fringe probably belongs to this variety. The specimen has near the cheek lobe 3 rows of small pits radially arranged. Lower portion of cheek-roll with irregular rows of pits. Brim with radial sulci.

(*Trinucleus*) *bucklandi* described by BARRANDE (1852 p. 621, Pl. 29, Fig. 10—17) shows a close resemblance to the above described variety. The good illustrations by BARRANDE make it possible to assume that the Bohemian species is identical with the variety of *T. granulata*. Bohemian material has not been present for a detailed comparison.

Provisionally the variety has received the name of the species described by BARRANDE.

Occurrence. The variety occurs in Sweden in Västergötland and Scania in the red and grey Trinucleus shale. On Bornholm it is found in the Trinucleus shale.

In Norway only a single fragment of the variety has been found in a horizon very poor in fossils in the upper part of the lower Trinucleus shale at Nakholmen, Oslo.

In Bohemia the variety is found in D_5.

For the present the species *T. granulata* seems to have had a western distribution while *T. granulata* var. *bucklandi* had a more eastern distribution.

GENERAL PART

Ontogeny of the Trinucleidae.

In the systematic part a detailed description has been given of the larval stages of Trinucleidae examined. Besides the known Meraspid stages of *Cryptolithus* described by BARRANDE (1852), BEECHER (1895), and BANCROFT (1929), larval stages of the genera *Trinucleus, Reedolithus* and *Tretaspis* have been described. The late Meraspid stages of *Tretaspis* are however mentioned by BARRANDE (1872). The preservation of the material used by BARRANDE is not very good for details. This is probably the reason why ocular ridges are not visible. I had the opportunity of examining a material from Bohemia of an ontogenetic series of *Cryptolithus ornatus* in the Riksmuseum in Stockholm. The stages agree with BARRANDE's drawing.

Of *Cryptolithus* all Meraspid stages from o—6 are known. No Protaspid stage is described. The specimens of St. O of *Tretaspis seticornis* seem to have had a very thin test. It is bent and deformed. This indicates that the test of the Protaspid stage probably has been too thin or soft for preservation.

Our knowledge of the early stages of the Trinucleidae shows a common, young stage which seems to have the same morphological characters within the different genera. The general characters might be summed up:

Body very broad, with long, rather broad genal spines. Cephalon with narrow, carinate, strongly elevated median glabella without glabellar furrows. Well developed median eye tubercle. Alar fields. Ocular ridges with faint eye-tubercles. Fringe consisting of two lamellae separated by a marginal suture independent of the eye-tubercles. Pygidium segmentated with badly marked rachis. The details of the larval stages are described in the description of the different species (p. 28, 34, 58 etc.).

Comparing the young stages of Trinucleidae with those of other Trilobites we find little correspondence in the oldest Trilobites.

The lack of distinct glabellar furrows is the chief difference. The greatest resemblance is found in a high phyllogenetic stage of development (WARBURG 1925 p. 30).

The Protaspis of *Corydocephalus consanguineus* CLARKE shows resemblance to the earliest Meraspid stages of the Trinucleidae.

Stratigraphical remarks on the Scandinavian Trinucleidae.

The Trinucleidae occur in Scandinavia in the middle and upper Ordovician. In Norway BRØGGER (1887) made a careful study of this formation in the Oslo district. HOLTEDAHL (1909) has described the same layers in the Mjøsen district, but only one species of Trinucleus is found there.

BRØGGER divided the formations into a number of zones. The Trinucleidae were partly employed as leading forms.

KIÆR (1920 p. 116) gives a new division of the Ordovician in the Oslo field. Three series are separated: lower, middle and upper Ordovician. The middle represents the Chasmops group. The upper, the Trinucleus-Isotelus group.

In Sweden the middle and upper Ordovician have been studied by several authors who will be mentioned below. The Trinucleidae characterizes some zones.

The earliest appearance of the family Trinucleidae in Scandinavia is in the lower part of the Ogygia (= Ogygiocaris) zone. Only species of genus *Trinucleus* are known from these beds. In the Oslo district of Norway the lower beds of the zone *Ogygiocaris dilatata* contain *Trinucleus foveolatus*. The present specimens are usually referred to the Ogygia shales without further details. My own collections seem to indicate an age of lower Ogygia shales. The Swedish specimens of *Trinucleus foveolatus* described by HADDING (1914) as *Trinucleus coscinorinus* were found in the lower Ogygiocaris zone.

In the middle of the Ogygia zone at Oslo scattered specimens of *Trinucleus bronni* are found. As mentioned above many specimens show a resemblance to the *foveolatus* type. The typical *Trinucleus bronni* is found in the upper part of The Ogygia zone. The species occurs abundantly in the sandy layers at the top of the shale. The zone is very distinct. It can be seen at Engervik in Asker and on the island of Killingen near Bygdø, BRØGGER (1887 p. 17) quotes the species from the lower part of the Ampyx limestone. In Sweden FUNKQUIST (1919) has separated a *Trinucleus bronni* (= *coscinorinus*) zone in Scania. He has made a stratigraphical correlation of the different localities. His table (p. 47) is partly built on the studies of HADDING (1914). The specimens of HADDING, determined by him as *T. bronni* (= *coscinorinus*) from the lower Ogygiocaris zone probably belongs to *T. foveolatus* (p. 16). The zones were correlated and the zone with *T. bronni* thus became a too old age.

The zone with *Trinucleus bronni* is probably equivalent in Norway and Sweden and represents a distinct stratigraphical horizon above the zone with *Ogygiocaris dilatata*.

Trinucleus bucculentus is found in the Ogygia shales, but its stratigraphical range is not well known.

In the Ampyx limestone above the *Trinucleus bronni* zone, *Reedolithus carinatus* is found. At Ringerike the rock succession of these zones has not been studied in detail. *Trinucleus bronni* occurs in layers probably of the upper Ogygia zone corresponding to the bronni zone. In the Ampyx limestone *Reedolithus carinatus* and *Trinucleus hibernicus* var. *broggeri* are found. I have recognised the first species in the collections from Jämtland, Sweden.

It is of interest to compare the said zone with those in Great Britain. In a recent paper, Ellis (1922) gives a review of the different stratigraphical horizons of the Bala country. The Llandeilian is well bounded upwards. The base of caradocian is characterised by *Dicranograptus clingani.* According to Olin (1911 p. 75) the species is also characteristic of the base of the Swedish Chasmops layers. The Ogygia and Ampyx layers below must thus be assumed to have a Llandeilian age. This also agrees with the Trinucleidae occurring in Llandeilian in Great Britain.

In Wales and Ireland *Trinucleus fimbriatus* Murch. is found which resembles *T. foveolatus.*

In Ireland *T. hibernicus* is very similar to the Norwegian variety. *Reedolithus subradiatus* resembles *Reedolithus carinatus.* Besides the said species some forms belonging to the genus *Cryptolithus* according to Stetson (1927 p. 88) are found. In the U. S. A. the Normannskill shows resemblance by the species *Reedolithus reticulatus.*

Trinucleus (?) *diademata* is doubtful in spite of the general resemblance to *T. foveolatus.* Ulrich (1930 p. 50) mentions forms similar to *Reedolithus subradiatus* in America. The age of the layers is above the Chagyan. The chief part of the Chasmops layers in Scandinavia corresponds to the Caradocian.

In Great Britain the Caradoc is rich in Trinucleidae. Ellis (1922 p. 163) regards *Cryptolithus tesselatus* (= *concentricus*) or a variety as one of the characteristic species of the Caradoc.

The lack of Trinucleidae in the typical Scandinavian Chasmops layers is probably due to the character of the fauna which shows many thick-shelled forms. The usual Trinucleid faunas are characterised by thin-shelled forms.

The base of the Ashgillian is clearly defined in the work of Ellis. In the general aspect of the ashgillian fauna she separates the *Phillipsinella parabola* beds below and the *Phacops mucronatus* beds above. She says p. 168: "*Phillipsinella parabola* appears both generically and specifically a characteristic form."

The species is found in the true Trinucleus shale and in the upper Chasmops limestone in Norway. Olin (1911) has also found *Phillipsinella parabola* in the Chasmops- and "Trinucleus"-zones of Sweden.

In Norway the upper Chasmops limestone is differently developed at Oslo and at Ringerike. At Oslo the top of the zone is indicated by a phosphoritic layer at the base of the dark Trinucleus shale (Kiær 1926 p. 17).

Raymond (1916 p. 244) suggests a break in the succession from the Chasmops — to the Trinucleus zones in the Oslo field, Kiær (1920 p. 121 and 1926 p. 17) mentions several bigger and smaller breaks between middle and upper Ordovician in the Oslo field. He assumes a smaller break between the upper Chasmops limestone and lower Trinucleus shale in the Oslo valley. The break is small in the S and SE of the Oslo field, and increases in the N and NW.

At Ringerike more layers of limestone are developed above the top layers of the upper Chasmops limestone at Oslo. On Bjerkø in Asker a transition stage is found. At Ringerike a chiefly unbroken sedimentation seems to have occurred from the Chasmops to the Trinucleus layers. In the upper part of the Chasmops layers *Tretaspis cerioides* is found. It is just below the typical layers with large *Echinosphaerites* sp.

Some meters above *Tretaspis kiæri* occurs. This is called the lower Trinucleus limestone. The zone was discovered and carefully examined by Kiær (1922, p. 499). One meter above the zone with *T. kiæri*, *Tretaspis seticornis* is found indicating the typical Trinucleus shale. Near Oslo *Tretaspis cerioides* var. *angelini* is found. The layer with *Tretaspis kiæri* is probably represented by a break, as suggested by Kiær (1922). *Cryptolithus dicors* is also found in the upper part of the Chasmops limestone. The distinct layer has not been traced with certainty.

The ashgillian fauna of Great Britain is inter alia characterized by the genus *Tretaspis* with the species *seticornis* and *granulatus* (= *bucklandi*). This, together with the appearance of *Phillipsinella porabola*, leads to the assumption that the lower limit of the Ashgillian must be found in the upper part of the Chasmop series (middle Ordovician) in Scandinavia. No change in the petrographical characters is found in the upper Chasmops limestone of Norway. The Trinucleus shale has a very different thickness. Near Oslo e. g. at Nakholmen it is little developed. (Brøgger 1887 p. 24).

At Ringerike the shale and limestone with *Tretaspis seticornis* are very prominent, (beautifully exposed in the west of the Island of Frognø). In Sweden similar black shales are known from Dalarne and Östergötland. At Västergötland *T. seticornis* is found at the base of the Trinucleus shales. The shales chiefly consist of green and red shales with *Tretaspis granulata*, and the var. *bucklandi*.

Kand. Junge, who has examined the Trinucleus shales of Västergötland, kindly informed me that in the highest layers of the shales *Tretaspis latilimbus* were most abundant. This is also indicated by Linnarsson (1869 p. 48). Apparently three zones exist in the Swedish Trinucleus

shales, lowest zone with *T. seticornis*, middle zone with *T. granulata* + var. and upper zone with *T. latilimbus*.

The seticornis zone is well known from Norway. I have tried to find *T. granulata*. Only one fragment has been found in the upper part of the black Trinucleus shale at Nakholmen near Oslo. In my opinion the Tretaspis granulata zone which is well developed in Västergötland and in Girvan, Scotland, is practically not developed in Norway. The beds, however, are very poor in fossils. In the Trinucleus shales of Scania and Bornholm the zone with *Tretaspis granulata* var. *bucklandi* is most prominent. The zone D_5 in Bohemia also seems to represent the same zone.

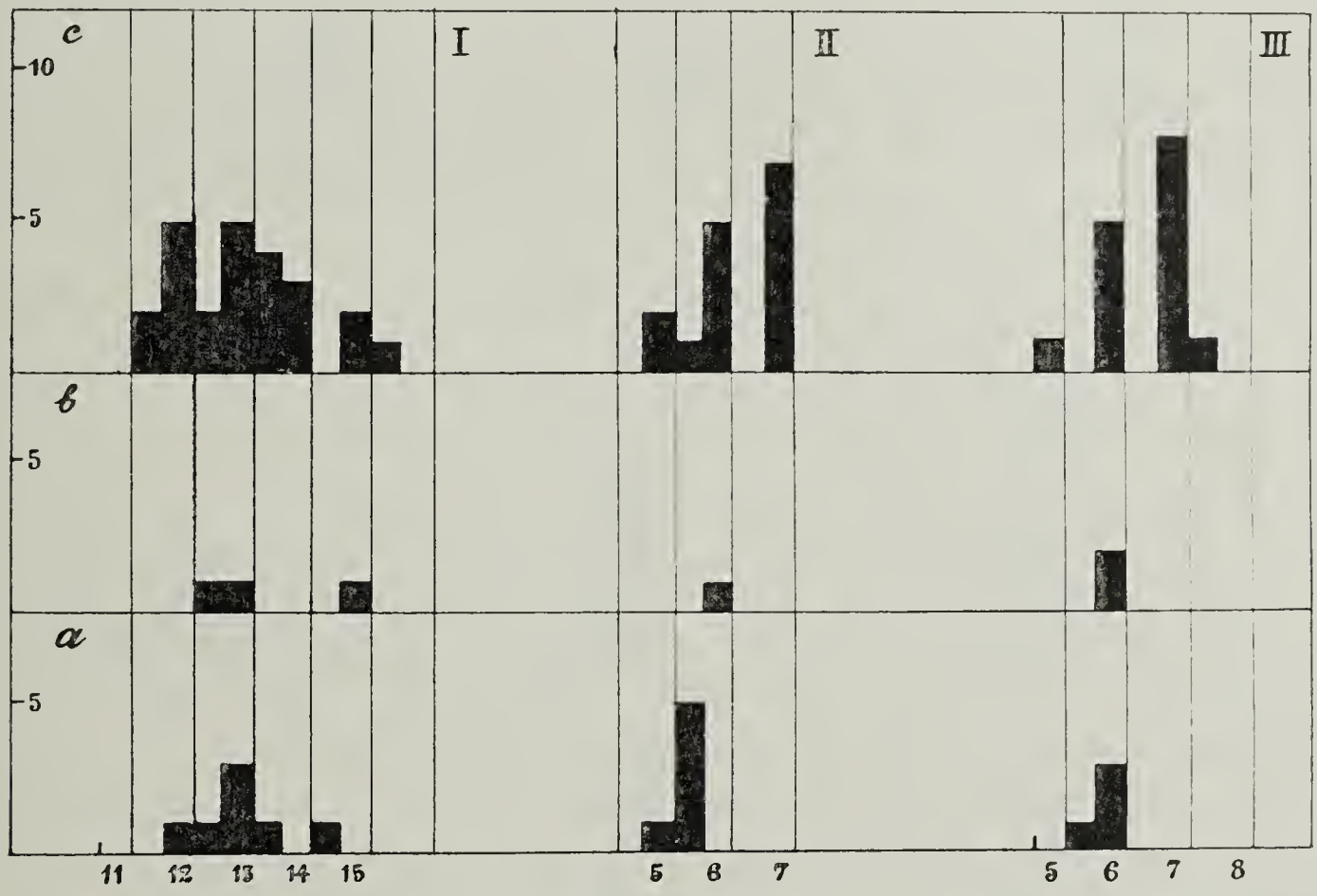


Fig. 32. Variation in the number of pits on the fringe of *Tretaspis granulata* (WAHL) and the var. *bucklandi* (BARR.). The upper graph (c) indicates a mixture of two forms. From the Trinucleus shale. *a* from Bornholm, *b* from Scania, *c* from Västergötland. Explanation of graphs on p. 10.

In the Trinucleus limestone near Oslo, some meters above the layer with the fragment of *Tr. granulata*, another form of *Tretaspis* occurs. BRØGGER (1887 p. 26) states *Tretaspis (Trinucleus) seticornis* HIS (?) var. In a foot-note he indicates the resemblance of the form to *Tretaspis latilimbus* LINN. My studies of the specimens of this layer show the close resemblance to the Swedish *Tretaspis latilimbus*. The graphs of Fig. 33 and Fig. 34 from the Swedish and Norwegian strata are quite in conformity. According to this, the Trinucleus limestone at Oslo must be correlated with the upper part of the Trinucleus shales of Sweden. The zone with *T. latilimbus* is not clearly defined at Ringerike. *T. seticornis* is found up through the Trinucleus shales and limestone. At the top, in the

transition layers of the Isotelus limestones, two specimens determined as *T. latilimbus* are found. KIÆR (1897 p. 35) mentions the species (called *Trinucleus Wahlenbergi*) from the Isotelus layers at Ringerike. At Oslo BRØGGER (1887) separated several Ashgillian zones above the Trinucleus limestone. He separates an upper Trinucleus shale, 3 zones with *Isotelus* and an upper zone with *Chasmops* — the typical gastropode limestone. The four lower zones are mainly based on petrographic characters. Very few fossils occur. The layers (e. g. exposed on the N. Langø in the Bundefjord) consist to a certain extent of sandy layers indicating a rather rapid sedimentation.

In the Trinucleus limestone *Isotelus* is found together with *Tretaspis latilimbus*. Through the zones of Isotelus *Tretaspis* cnfr. *latilimbus* is found. In the upper zone with *Chasmops*, the gastropode limestone, *Tretaspis latilimbus* is common. Fig. 33 gives the graph of the form. The difference from the Trinucleus limestone form is too small to suggest a new variety, but the two graphs do not quite conform.

BRØGGER (1887 p. 33) reports *Dalmanites mucronata* from the upper zone. This is discussed by KIÆR (1897 p. 32). According to TROEDSON (1918 p. 29) the zone must be correlated with the brachiopode shale of Sweden.

Tretaspis latilimbus occurs in the Trinucleus limestone and at the base of the gastropode limestone (upper Chasmops zone). This together with the sandy layers of the Isotelus beds indicates a short time of sedimentation of the Isotelus zones. In my opinion the Isotelus layers are closely connected with the Trinucleus shales and limestones.

The black Trinucleus shale of Oslo measuring 6—7 meters probably corresponds to the large thickness of the Trinucleus shales and limestones at Ringerike, and to the seticornis and granulata zone of Sweden.

The Trinucleus limestone, upper Trinucleus shale and the three Isotelus zones seem to represent a relatively short space of time. It must be correlated with the upper part of the Trinucleus shales of Sweden.

In the upper Chasmops zone a species of *Cryptolithus* is found near Oslo.

According to TROEDSON 1918 p. 30 the upper Chasmops zone (equivalent to the brachiopode shale of Sweden) must be of the same age as the middle Ashgillian. It represents the upper part of Ashgillian in the division of ELLIS 1922 p. 164 represented by *Phacops (Dalmanites) mucronatus*.

The detailed stratigraphical correlation of the different countries will not be established in this paper.

The different zones containing Trinucleidae can be summed up in the following. The correlation must be confirmed by a detailed study of the faunas.

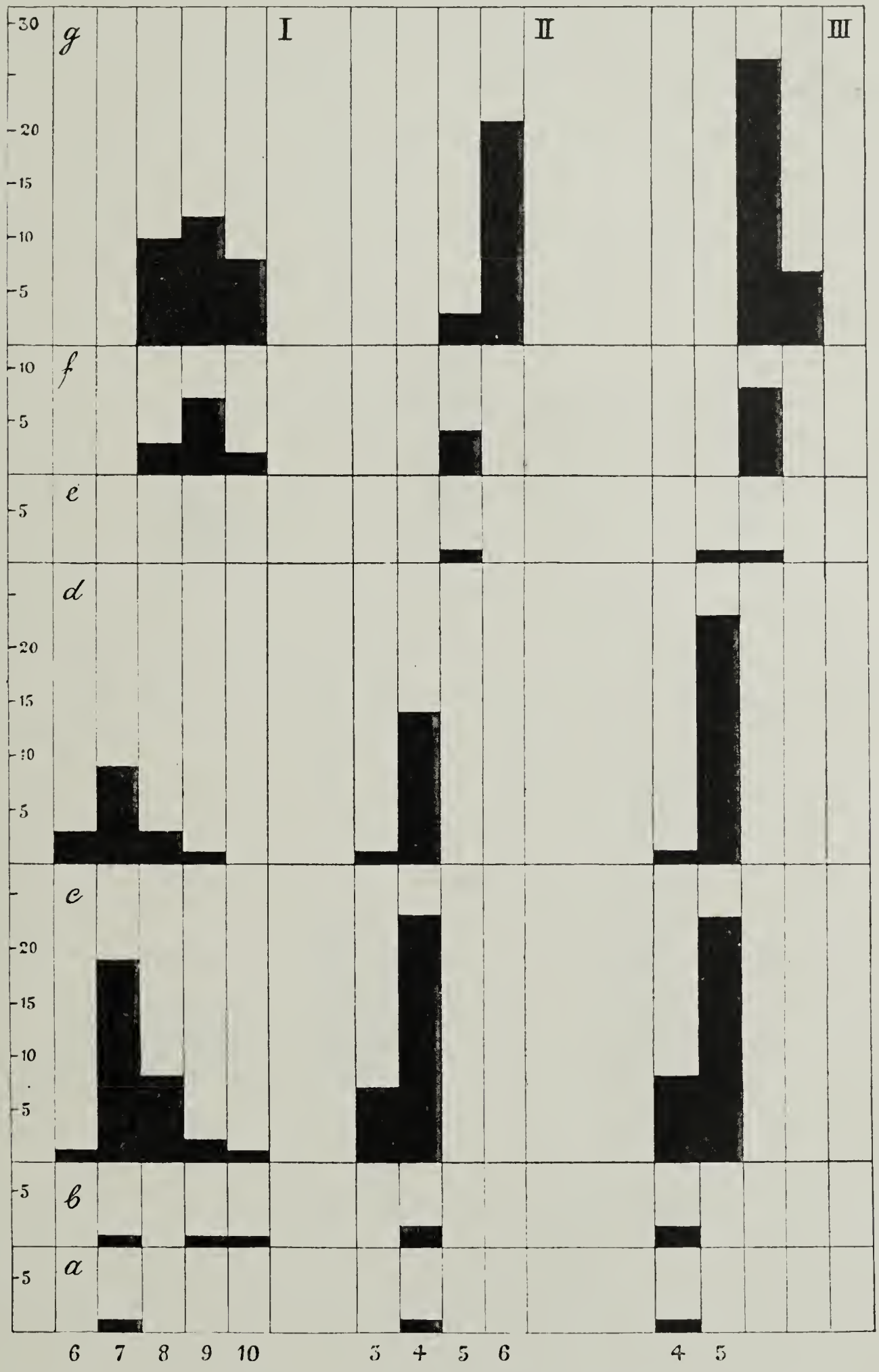


Fig. 33. Variation of the number of pits on the fringe of late Norwegian *Tretaspis*. *a* – *d* = *T. seticornis* (His), *e* – *f* – *g* = *T. latilimbus* (Linrs.) *a* from upper part of low. Trinucleus limestone. *b* middle Trinucleus shale, *c* upper Trinucleus shale, *d* lower part of upper Trinucleus limestone, *e* upper part of upper Trinucleus limestone, *f* Trinucleus limestone, *g* the upper Chasmops zone. *a*—*e* from Frognø, Ringerike, *f* from Lindø, Oslo, *g* from the islands of Oslo.

Explanation of the graphs p. 10.

Zone with	*Tretaspis latilimbus*	Ashgillian.
—„—	— *granulata* + var.	
—„—	— *seticornis*	
—„—	— *kiæri*	
—„—	— *cerioides* + var.	
		Caradocian
—„—	*Reedolithus carinatus*	Llandeilian.
—„—	*Trinucleus bronni*	
—„—	— *foveolatus*	

Phyllogeny of the Trinucleidae.

In a recent paper Stetson (1927) gives an interesting account of the Trinucleidae. He has grouped all known Trinucleidae in the 3 genera proposed by Raymond. The large number of species are to a great extent little known. The descriptions and illustrations are often very incomplete. The stratigraphical position has also often not been exactly determined. The Scandinavian forms were little known, and Stetson received a partly wrong impression of their structure and stratigraphy.

The phyllogeny of the Trinucleidae is based on the stratigraphical appearance, the morphological characters, and a study on the ontogeny.

The studies of Stetson (1927 p. 98) show the wide geographical range of the species of the family. The same or allied species occur in allied strata at very different places. A long geological range is only found among the species of the genus *Cryptolithus*, but this is to a great extent due to the great difficulties in the systematic classification of the species of that genus. The Trinucleidae are good index fossils.

The morphological characters of the species seem to have different values as phyllogenetic indicators. The value must be regarded with a background of the appearance of the different morphological characters during the general ontogenetic development of the Trinucleidae.

The law of Dollo which says that rudimentary organs never reach the original strength, and obsolete organs never again appear during the evolution of the stock, might be used in regard to phyllogeny.

The origin of Trinucleidae has been discussed by several authors, e. g. Lake (1907 p. 44), Swinnerton, (1915, p. 489), Reed (1916, p. 175), Raymond (1917, p. 203) and Stetson (1927, p. 94).

Lake, Swinnerton and Reed state *Orometopus* as an ancestor of the Trinucleidae. The species occuring in the Tremadoc shows great resemblance to the Trinucleidae in "the clavate glabella, the horizontal grooved pleurae and the broad triangular tail." (Lake 1907, p. 44). *Reedolithus carinatus* shows in younger stages a great resemblance to *Orometopus*. To the characters mentioned by Lake might be added: The glabella is often carinate (Brøgger 1882 Pl. 3, Fig. 13). A median tubercle is present

(Størmer 1920 Fig. 3). Alar fields occur. The characters show a great resemblance to the Trinucleidae. In my opinion the shape of the *Orometopus*-like stage of *Reedolithus carinatus* is due to a free swimming mode of life. The question whether the resemblance to *Orometopus* is due to a similar mode of life, and thus only a phenomenon of convergence, or is due

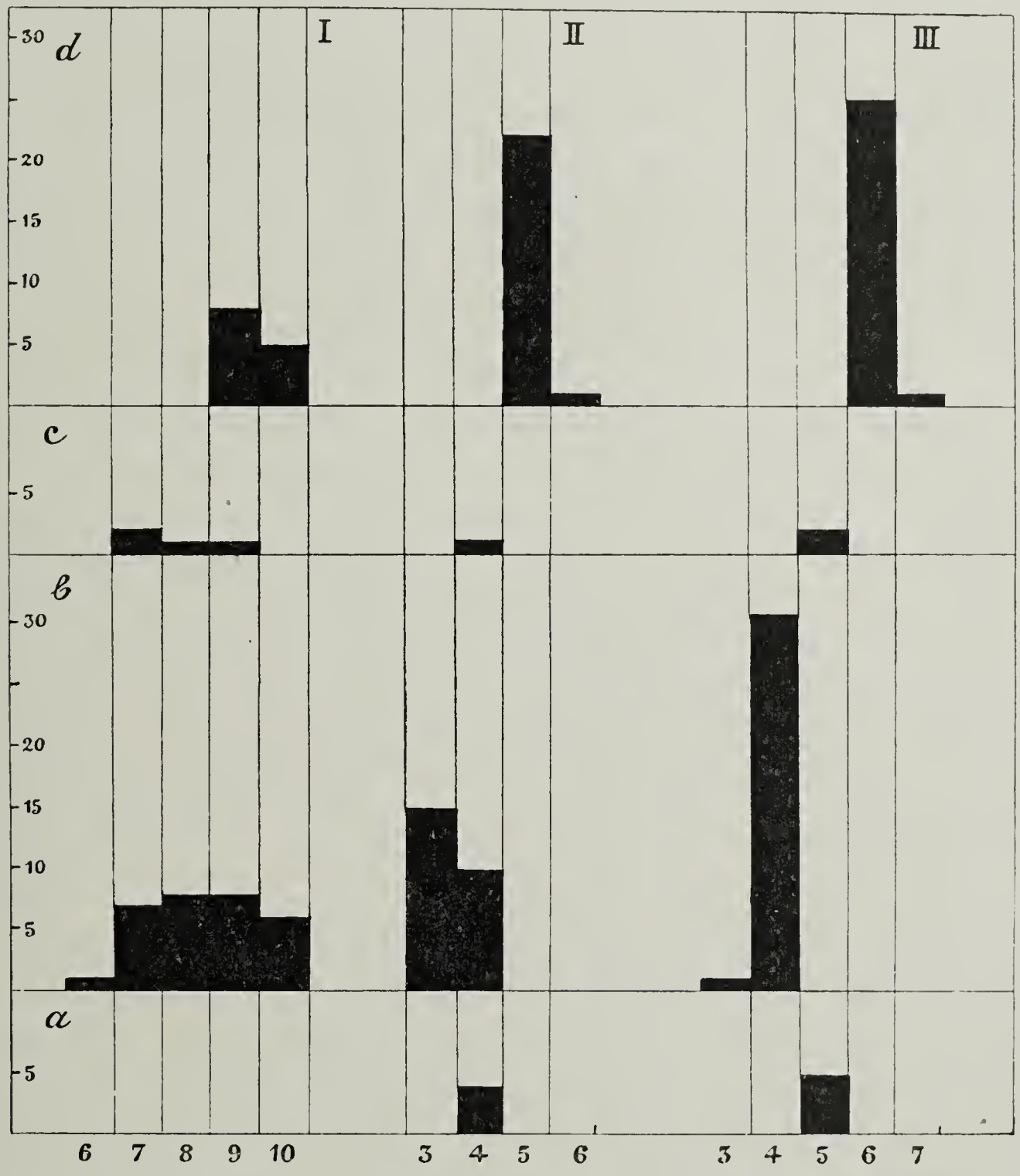


Fig. 34. Variation in the number of pits on the fringe of Swedish *Tretaspis* (comp. Fig. 1). *a* = *T. cerioides* (Ang.)? from grey limestone below the Trinucleus shale in Västergötland. *b* = *T. seticornis* (His) from Trinucleusshale in Östergötland. *c* = *T. seticornis* (His) from Trinucleus shale, Öland. *d* = *T. latilimbus* (Linrs.) From upper part of the Trinucleus shale Västergötland. Explanation of graphs p. 10.

to an indication of descent, is difficult to decide. Raymond and Stetson refuse the relationship with *Orometopus*. Raymond (1917 p. 293) calls attention to the greater number of segments in *Orometopus*, but this need not be of great importance since *Harpes* has been proved to be related to *Trinucleus*. Raymond and Stetson indicate an isopygous group like the Eodiscidae to be the ancestor. This is probable if an ancestor of trilobites with few or

no thoracic segments is assumed. If an ancestor with several thoracic segments is assumed, a reduction of the number of thoracic segments is hardly followed by a new increase in the number as would be the case from *Microdiscus* to *Trinucleus*.

The Arenig species of Trinucleidae belong to *Trinucleus* and *Cryptolithus* (?). Both genera have a well developed fringe. This is especially prominent in the *murchisoni-etheridgei* group of *Trinucleus*. The little known *Cryptolithus (?) primitivus* (Born) (Fig. 35) from France, (Born. 1921) has a broad lateral portion of fringe with numerous irregularly arranged pits. It is like the young stage of *Reedolithus carinatus* (Pl. 5, Fig. 1).

Earlier authors have always regarded the narrow fringed forms as the most primitive. This is founded on the ontogeny which shows the earliest Meraspid stage with narrow fringe practically without rows of pits.

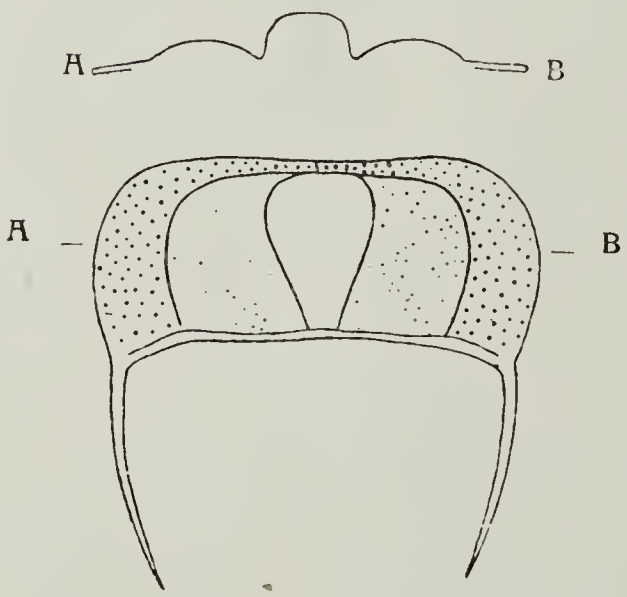


Fig. 35. *Cryptolithus primitivus* (Born). (Reproduced after Born, Fig. 1).

The present knowledge of the ontogeny shows that the fringe is well developed at very early larval stages, corresponding to a length of 1 mm of cephalon. This indicates an old origin of the fringe. In the geological range the fringe is also rather well developed in the early, Arenig species. The later forms with narrow fringe have probably a mainly reduced fringe.

From Llandeilo several species of *Trinucleus* are known. The *foveolatus — bronni* group shows primitive features in the lack of genal prolongations of fringe. The same was found in the probably allied form in Arenig, *Trinucleus gibbsi* Salter.

The shape of the cephalon and glabella of *Trinucleus foveolatus* is like the larval stages of Trinucleidae. This probably indicates primitive characters. The transition forms between *T. foveolatus* and *T. bronni* from older to younger layers mentioned on p. 29, indicate a reduction of fringe. It cannot be definitely decided. They may belong to different branches of descent. *T. hibernicus* and *T. bucculentus* must be regarded as specialised forms with reduced fringe. The latest member of the genus *Trinucleus* is represented by *Trinucleus albidus* in Caradoc.

In Llandeilo the species of *Reedolithus* appears. *R. reticulata* is not sufficiently known to decide if it is a *Reedolithus* or an early *Tretaspis*. The former is most probable. *Reedolithus* shows primitive characters in the carinate glabella without pseudo-frontal lobe. The occipital spines and the concentric arrangement of pits indicate a descent from early *Cryptolithus* species (confr. Ulrich 1930 p. 50). The lateral eyes are of little phyllogenetic value. The slow ontogenetic development of *R. carinatus* could be regarded as a primitive feature. As mentioned on p. 107 this is probably

due to the free swimming mode of life similar to the younger stages of the other genera. The oldest specimens show a remarkable resemblance to *Tretaspis* in the shape of fringe and glabella. This is a good proof of convergence in the evolution of the Trinucleidae and shows the great difficulties in the determination of relationship and descent. *Reedolithus* is probably represented in Caradoc by *R. radiatus*.

The genus *Cryptolithus* is known from Arenig up into Ashgillian. The line of descent is suggested by STETSON (1927 p. 95). I do not think it probable that the Llandeilian species have descended from the *gibbsi-sedgwicki* group of *Trinucleus* which has a narrow lateral fringe and radial arrangement of pits. The genus *Cryptolithus* has its chief development in Caradocian.

The genus *Cryptolithus* is replaced by *Tretaspis* in the Ashgillian. STETSON (1927 p. 96) mentions several Scandinavian species from Caradocian. As above discussed, (p. 76) they must probably be placed at the bottom of Ashgillian. *T. seticornis,* var. *portrainensis* REED (1897 p. 538) from Ireland was found in layers referred to Bala. correlated with the Sholeshook limestone of South Wales.

The genus *Tretaspis* probably first appears in the Ashgillian. As emphasized by STETSON (1927 p. 96) no certain ancestor can be pointed out in the older layers. Using the law of Dollo we can scarcely expect to find a form with a rather broad fringe as a descendant of forms with a reduced fringe. It cannot be decided if the narrow fringed *Trinucleus,* which shows resemblance to *Tretaspis*, does not have reduced fringe. If they are forms with reduced fringe, they can not be regarded as ancestors of the genus *Tretaspis*.

The Scandinavian material gives good conditions for studying the evolution of the genus *Tretaspis*. We can trace several branches of evolution. The stratigraphical position is determined for the different species.

One branch is indicated in *T. cerioides* → *T. kiæri* → *T. granulata*. The evolution consists of an increase of size and complication of fringe. The number of rows of pits and the genal prolongation increase.

The graphs Fig. 21, p. 45, Fig. 32, p. 77 show the facts.

A second possible branch of descent is noticed in *T. seticornis* → *T. latilimbus* → *T. latilimbus*. The late *T. latilimbus* is found higher up and shows a few more pits on the fringe than the lower one. The fringe is broader in *T. latilimbus* than in *T. seticornis*. The graphs Fig. 33 show the facts.

T. cerioides var. *angelini* seems to be the most primitive *Tretaspis*. It has a faintly developed pseudofrontal lobe and slightly differentiated glabellar furrows.

The median Eye-tubercle.

Among the Trinucleidae and several other families of trilobites a small pustule or tubercle is found on the glabella.

Barrande (1852 p. 616) mentioned it with regard to *Tretaspis bucklandi*. The tubercle is visible in drawings of *Tretaspis, Trinucleus* and *Cryptolithus* by Angelin. (1851—54).

The various earlier authors have not given any definite explanation of the presence of the pustule, but suggested several functions for it.

Beyrich (1846) considered the tubercle as a beginning of the alimentary canal. Bernard (1894) compared it with the dorsal organ of *Apus*. McCoy (1856) mentioned it as an ocular(?) tubercle.

Oehlert (1895, p. 340) says that the median tubercle indicates a 3rd simple eye in concurrence with the two lateral ones.

Beecher (1895 b) states that although its nature has not been demonstrated it has been considered an ocellus.

Reed (1916 p. 175) suggests a "dorsal organ" of phyllopods or a median unpaired ocellus.

He also considered it to be connected with the "dorsal organ" of *Apus*.

Ruedemann (1916 a) has given a valuable addition to our knowledge of the subject in his paper: "The presence of a median eye in Trilobites". He has made a detailed study of the median tubercle of *Cryptolithus* and gives a review of all known trilobites with a median tubercle on the glabella. He came to the conclusion that the median tubercle represents a true median or parietal eye as is found in crustacea. His sections of *Cryptolithus* and *Asaphus* showed a thin shell above the ocellus. A small lenticular body was found below the shell. Richter (1921 a, p. 105) has suggested the origin of the lenticular body as a late filling of an empty cavity. In the Norwegian material several cases of different stages of calcite filling below the glabella and eyes have been recognized (See Pl. 14, Fig. 1). No lense in the median tubercle was found by Ruedemann. This indicated a relationship with the phyllopodae. The fact that young *Isotelus* and *Cryptolithus* (p. 135—136) show a relatively large tubercle compared with that of the mature stage also suggested a median eye. The smooth tubercle on the top of the glabella between the lateral eyes was probably a visual organ. Ruedemann calls attention to the presence of a median eye in primitive crustaceans and merostomes.

Raymond (1920 p. 87) comes to the conclusion in his wellknown paper on "appendages anat. etc." that the median tubercle does not represent a median eye.

His chief arguments against the median eye are as follows: The tubercle is like the several other tubercles on the thorax and pygidium. The thin shell of the tubercle is found in all tubercles of the cephalon of

Ceraurus. The lenticular body can be explained as belonging to different organs. The position of the tubercle varies greatly. The median tubercle is in many cases developed into a long spine comparable with the zoael spine in recent crustacea. *Trinucleoides reussi* (BARRANDE) was probably a swimmer with a balancing spine. This was reduced later when the Trinucleidae became burrowers.

Finally he mentioned the unexplained feature that no "Nauplius eye" is found in the protaspis. BEECHER (1897 a, p. 40) explained it as due to imperfect preservation. RAYMOND says (p. 89) "If the med. tubercle was really a median eye, it should be present in the protaspis and the earlier stages of ontogeny".

HANSTRØM (1926) agrees with RUEDEMANN in the explanation of the tubercle being a median eye. He suggests the possibility that the median and lateral tubercles of *Tretaspis* represent 3 components of a median eye. A division of the median eye is found among the copepoda.

In the Norwegian material a median tubercle is found in the 4 genera: *Trinucleus, Reedolithus, Cryptolithus* and *Tretaspis*. With the exception of the first, all genera have lateral tubercles.

The median tubercle is always found on the top of the glabella, ɔ: on the pseudofrontal lobe. In the present specimens of the Trinucleidae only a few show the outer surface of the shell. Usually only the inner cast of the cephalon is preserved. Several sections have been made in order to study the shape and structure of the tubercle. Like the lateral tubercles the median ones vary within the genera. Species with a nearly smooth surface of the glabella have an only slightly elevated tubercle (*Tretaspis seticornis*). Highly reticulated forms show strongly elevated tubercle (See Pl. 13, Fig. 3) (*Tretaspis kiæri*).

Among the genus *Trinucleus, T. bucculentus* shows a very distinct median tubercle. The section (Pl. 13, Fig. 4) shows the rather strongly elevated tubercle. In *T. foveolatus* it is small and very like that in *Cryptolithus*. The tubercle is not very well separated from the rest of the surface of the glabella. In *Cryptolithus* the small tubercle is very distinct.

Morphology of the median tubercle.

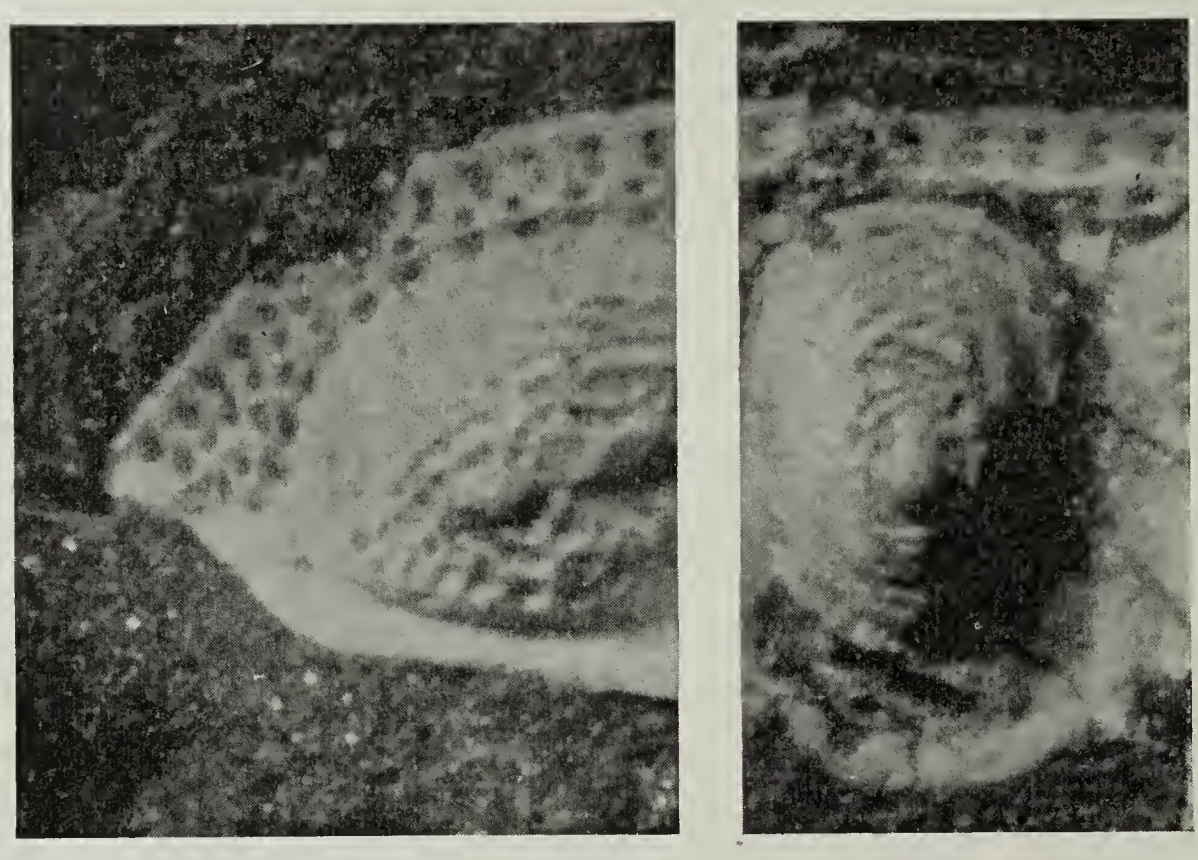
The median eye tubercle has been studied in detail in *Tretaspis*. Very seldom the upper surface of the shell of the glabella with the tubercle is well preserved. In 3 specimens the minute structure of the median tubercle can be studied:

The first is a specimen (12. e.) of the 2nd. Meraspid stage of *T. seticornis* from the Trinucleus shales in Dalarne, Sweden, (Pl. 7, fig. 9 and text Fig. 36, 37).

The cephalon measuring 1.0 mm in length has a white test quite different to the black matrix of the shale. The specimen was found when

the pieces of slate were split, therefore the surface is not weathered. The specimen is beautifully preserved in spite of the pressure. On the top (centre) of the glabella a large semispheric tubercle is seen. The tubercle is well limited by the reticulated surface of the glabella.

The even smooth surface of the tubercle is interrupted by 5 small distinct impressions. 5 quite small pits arranged in a square with the 5th pit in the centre. The lateral sides of the square are paralell to the median line of the trilobite. The impressions have been examined very carefully greatly magnified. It seems impossible that they belong to occasional accidental impression. A minute study of the pits in the corners of



a b

Fig. 36. *Tretaspis seticornis* (His) × 50. Meraspid stage II showing median and lateral eye tubercle. *a* = 12 g, *b* = 12 e. Trinucleus shale Dalarne. (Törnquist coll. Geol. Inst. Lund).

the quadrangle shows no black spot in the bottom indicating a perforation of the specimen. The central pit has a black spot at the bottom suggesting a perforation to the black slate matrix below. This pit has been recognised in another specimen of the same stage.

The two other specimens represent adult stages of *T. seticornis* from the upper Trinucleus limestone at Ringerike, Norway. Pl. 11, Fig. 5, 7 show the glabella surfaces with the tubercles. The reticulation is quite reduced in H 100. This specimen is photographed posterio-dorsally.

The tubercles (Fig. 37 c—d) are gently arched, buttonshaped pustules. The outline is not quite circular. The diameters are 0.18 and 0.26 mm.

A minute study of the surface shows some small impressions. Besides some small assymetric ones, 5 more distinct pits are seen. They are bilaterally and partly radially arranged. They make a deformed square

with a central pit. The central pit is distinct in H 103 but damaged in H 100. The 4 pits in the quadrangle are more or less distinct. The small pits are shallow and have a circular or oval outline. The position of the pits is seen in the drawings, Fig. 37.

The structure of the median tubercle in these adult specimens quite agrees with that of the larval stages.

Shell structure of the median tubercle.

It has been very difficult to obtain sections just over the small median tubercle. About 7 more or less good sections have been made.

The sections of *Tretaspis kiæri* show a slight difference in the colour of the test above the cavity of the tubercle (Pl. 13, fig. 3). Most attention

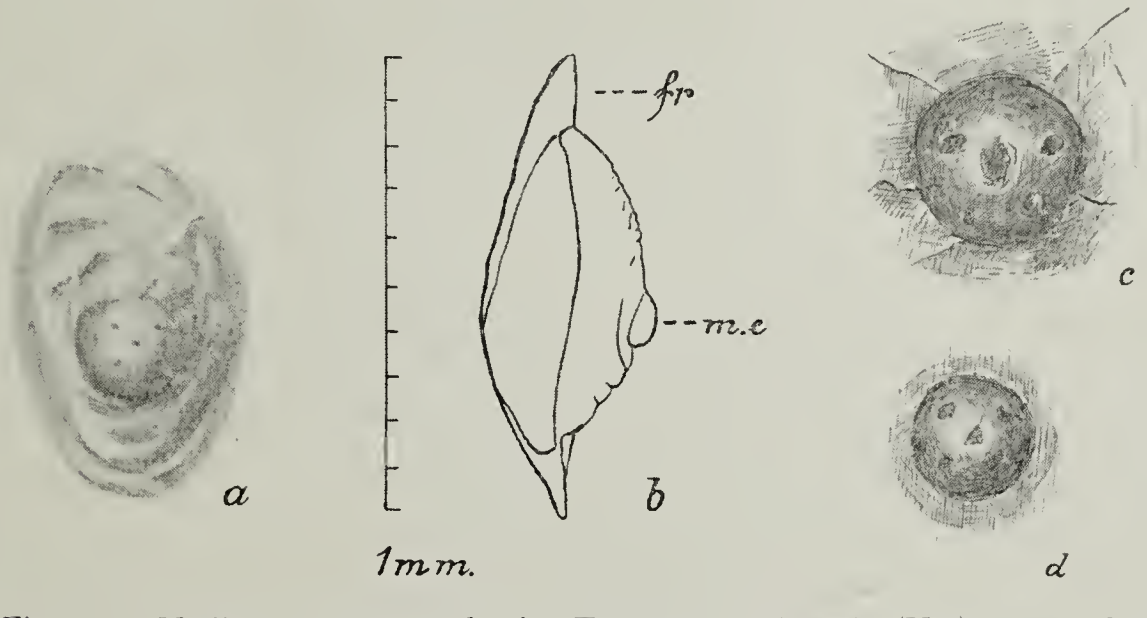


Fig. 37. Median eye tubercle in *Tretaspis seticornis* (His). *a*, × 80. *b*, × 36. *c*, *d* × 50. *a*, *c*, *d* showing 5 small pits on the tubercle. *a*—*b* Meraspid stage II. *c*—*d* adult. *b* Lateral view of cephalon with the big median tubercle. *a*—*b* from the Trinucleus shale Dalarne (12. e. Törnquist coll. Geol. Inst. Lund). *c*—*d* from the upper Trinucleus limestone Frognø, Ringerike (H 103, H 100 Kiær coll. Pal. Mus. Oslo).

has been paid to the FeS_2 — dyed slices of *T. seticornis* (Pl. 13, fig. 5, 6). No lense has been found. The pigment layer seems to disappear, but this may happen also in other places of glabella owing to a different kind of preservation. In Pl. 13, Fig. 6 a dark line in the centre of the tubercle is seen. The younger specimen Pl. 13, Fig. 5 shows no FeS_2 — filled canals. When highly magnified traces of a canal can be seen in the centre. Only the faint limits can be traced by the micrometric screw. The presence of a canal in the centre of the tubercle cannot be decided with certainty.

Ontogeny of the median eye.

The median eye which is found in all primitive arthropoda should probably exist in the trilobites. The above mentioned lack of the "nauplius" eye was assumed by Patten (1912) and Beecher (1895 a, p. 40)

to be due to the bad preservation. This is verified by the present material.

The median eye is preserved in the Meraspid stages of *Tretaspis seticornis* found in Dalarne, Sweden. Stage O had a too thin shell for a good preservation. In one specimen a rather big med. tub. is visible (Pl. 7, Fig. 3). In st. II where the shell is well preserved the size of the med. eye is somewhat larger than the little developed lateral eyes. Fig. 36 shows the size of the two different eyes. During growth the lateral eyes soon, at St. III—IV, reach the size of the median eye. In the later stages the lateral eyes fully exceed the size of the med. eye. (Compare Pl. 11, Fig. 5, 7 and Fig. 6).

It is of interest to compare the size of the med. tub. with the length of the cephalon. In the young specimen of 2nd Meraspid stage the diameter of the med. eye is 0.1 of the length of the cephalon. In the adult specimen the diameter is 0.028 in H 100 and 0.03 in H 103 of the length of cephalon. Relatively the size of the med. eye tubercle is 3.3 to 3.6 times as large in the adult. The surface is relatively reduced to $\frac{1}{11}$ to $\frac{1}{14}$ from the IIst. to the adult.

It is a general feature to find the median tubercle best developed in the younger stages. This is also found in *Trinucleus foveolatus* Pl. 1, Fig. 9, *Reedolithus carinatus* (Pl. 5, Fig. 3, 4). Beecher (1895) found it in *Cryptolithus tesselatus*.

The objections of Raymond concerning the tubercles as a median eye were amongst others the resemblance between the pustules and the tubercles on the cephalon and thorax. They show the same section with a thinning of the shell. I have made sections of the reduced spines from the head of adult *Limulus*, and found the same thinning of the shell. The particular structure of the med. tubercle with the 5 pits makes however a difference to the common pustules. The presence of the med. tubercle in the young larval stages makes it less probable that the tubercle represents a rudiment of a zoal spine. The larval were probably swimming and not crawling in the young stages. In *Reedolithus carinatus*, which seems to have been a swimming form up to the adult stage, the occipital spine probably served as a zoal spine. The med. tub. was well developed. The lack of the med. tub. in the larval stages was also used by Raymond against the assumption of a median eye.

The view of Hanström of the med. and lat. tubercles being 3 components of the median eye cannot be maintained since the med. tubercle shows a different minute structure.

The front tubercle, found by Ruedemann in *Cryptolithus tesselatus* (Ruedemann 1916 a, Fig. 4), has not been found.

Comparing the above-mentioned structures with those found in the med. eye of recent arthropoda great resemblance is found. In *Apus* (Patten 1912, p. 138) (Holmgren 1916) the median (pariatal) eye consists

of four distinct ocelli which have migrated from the sides during the development. PATTEN says: "They are enclosed in a common sac, which opens to the exterior by a short duct or pore". No lens occurs. This is different to the other arthropod ocelli (PATTEN 1912, P. 144). HOLMGREN (1916 p. 133) says: "In das Nauplius-Auge von *Apus* gehen also meiner Meinung nach nicht weniger als 5 Retinas hinein." He thus indicates that the ancestors of *Apus* might have had 5 retinas in the median eye. We have two ways in which to explain the pits on the surface of the median tuberble:

(1) The central pit represents the opening of the eye sac and the four pits in the quadrangle indicate the 4 ocelli.

(2) The 5 pits represent the 5 ocelli of which the 5th is reduced in recent phyllopoda.

The faint traces of a canal in the centre of the median eye, found in the sections, speak in favour of the first assumption.

The summary of results concerning the median tubercle is as follows:

The median tubercle found on the top of the glabella in several trilobites must be regarded as a true median eye.

The median eye has been found in 4 genera of Trinucleidae. It shows a different structure to the lateral eyes. The surface of the median eye shows 5 distinct impressions indicating 4 or 5 ocelli below. The structure resembles the recent phyllopoda. No lens is found as in the lateral eyes.

The ontogeny of the Trinucleidae shows that the median eye is highly developed in the early larval stages when the lateral eyes are small and little developed.

The Lateral eye of Trinucleidae.

In the literature the lateral tubercle on the cheek lobes of *Tretaspis* has been mentioned several times. Only some of the papers on the subject will be quoted. The nature of the tubercles has been regarded as an ocellular, or the Trinucleidae has been regarded as a blind form. RAYMOND (1913 b, 711) states "Ocelli and eye-lines" to the genus *Tretaspis*, but not to *Trinucleus*.

REED (1916, P. 174) says: "It may be here mentioned that no lenses have yet been detected in the so-called ocelli of any species of *Trinucleus* [Trinucleidae] though they are well developed in *Harpes* and are schizochroal. The visual function of these genal tubercles in *Trinucleus* is generally assumed, but it may be that they had some sensory function, or that their visual powers (if they are regarded as degenerate compound eyes) have become rudimentary." WARBURG (1925, p. 69) says about Trinucleidae and *Ampyx*: "Both are, as is well known, blind forms".

Richter (1921 b) made a careful study of the eyes of *Harpes*. He came to the conclusion that the eye of *Harpes* which consisted of two biconvex lenses is homologous to the normal lateral eye of Trilobites. He says: (p. 196) "ähnlichliegende Knötchen Larven und einigen Arten von *Trinucleus* (*Tretaspis*) werden ihnen *Harpes* einstweilen nur auf grund ihrer Lage ohnen Kenntnis des Baues gleich gestellt".

Walcott (1921, Pl. 104, Fig. 10) figures a slide of *Cryptolithus tesselatus* which shows a lateral eye with corneal lenses. Since the lateral eye tubercle is unknown in the adult specimen of this genus, the structures of section probably must be explained as a fine meshed reticulation on the surface of the test of the specimen.

The Norwegian Trinucleidae has given a good material for the study of the lateral eye tubercles. The tubercles are found in the genera, *Trinucleus, Reedolithus* and *Tretaspis*. In the larval stages of the genus *Cryptolithus*, Beecher (1895 b) found lateral tubercles.

The old British *Trinucleus* species show no lateral eye tubercle, only traces of ocular ridges. The lack might to a certain extent be due to inferior preservation. In the present material the lateral eye tubercles have been found in the species: *Trinucleus foveolatus* + var., *T. bronni*, *T. bucculentus*., *T. hibernicus* var. *broggeri*, *Reedolithus carinatus*, *Tretaspis cerioides* + var., *T. kiæri*, *T. seticornis* and *T. latilimbus*.

In the larval stages tubercles appear as small more or less differentiated nodules on the lateral end of distinct ocular ridges. (Fig. 14, 15, 35 and Pl. 4, Fig. 7, Pl. 5, Fig. 1, 3, Pl. 7, Fig. 1, 2, 3, 7, 10). The ocular ridges begin just behind the 1st pair of the glabellar furrows. According to Swinnerton (1919) the ocular ridges with the lateral eye are always connected with the 4th segment reckoned forwards from the occipital ring, In the larval stages the glabellar furrows are developed at a late stage.

The connection with a glabellar segment cannot be traced. The segmentation of glabella is probably lost after the Protaspid stage. The ocular ridges are often absent in the adult stage. They are most distinct on the internal cast, indicating a fissure in shell. The branched ridges situated laterally from the eye tubercle, called genal cecae, are found in *Trinucleus, Reedolithus* and *Tretaspis*. They are more or less developed. Raymond (1920 p. 84) has discussed the organs in *Cryptolithus*. Warburg (1925 p. 222) mentions it in *Tretaspis seticornis*. Earlier authors have connected it with the facial suture, but this does not seem to be the fact. It is homologous to the "nervures" found in other trilobites.

Fig. 36 shows a well preserved lateral eye tubercle at the 2nd Meraspid stage. The eye tubercle seems little developed. During the development the tubercle grows very distinct and well marked from the surrounding surface of the cheek lobe (Pl. 11, Fig. 6). The faint lat. tubercles of *Trinucleus foveolatus* show a great resemblance to the larval stages of

Tretaspis (Pl. 1, Fig. 10), but it is here probably a rudiment and not an oriment since the young stages show a well marked tubercle (Pl. 1 Fig. 9).

The lateral eye tubercles of *Reedolithus carinatus* show several features of interest. The posterio-lateral position is like that of the usual Meraspid stages. (The earlieast Meraspid stage seems however to have the lat. eye tubercles more medially). The lateral position of the eyes indicates a free swimming life. The lateral eye tubercles of *Reedolithus carinatus* are very large (Pl. 4, Fig. 12). The internal cast of the tubercle (Pl. 5, Fig. 10) shows a central thinning of the tubercle and a surrounding list. Similar features are perhaps the lobes surrounding the two lenses of the eyes of *Harpes*. (Richter 1921 b Pl. 17, Fig. 10). The young Eurypterida show similar shapes, (Clarke and Ruedemann 1912 Pl. 51, Fig. 1—6).

In the genus *Tretaspis* the tubercle is often strongly elevated (Fig. 24, p. 51, Pl. 13, Fig. 1, 2). The surface is quite smooth although the cheek lobes are strongly reticulated. (Pl. 11, fig. 6).

Several sections have been made to study the structure of the lat. tubercle. Pl. 12, Fig. 3 and Pl. 13, Fig. 1, 2 illustrate some of the sections of the tubercle in *Tretaspis seticornis*. Pl. 13, Fig. 2 belongs to a young specimen. The shell is thinner in the tubercle than in the surrounding cheek lobe. Just at the top the shell has a dark colour. The dark body has an arched lower surface. It appears quite like a biconvex body of a different structure to the remaining shell. The same structure is found in the two other sections, but not so remarkable. The darker body of the top of the tubercle of Pl. 13, Fig. 1 shows no extinction in crossed nicolls, opposite to the rest of the shell at the sides. The thin, dark, outermost layer of this section cannot for the present be explained. The dark biconvex body must be regarded as a true ocular lens. It is not traceable in most of examined sections, but the presence in the above mentioned 3 specimens fully shows its presence. The calcite-filled inner portion of the tubercle could be explained as an outline of the eye, but it is more likely that it is due to gases caused by putrefaction (See p. 50).

Richter (1921 b P. 1924) described the eyes of *Harpes*. In *Harpes* no thinning of the shell is found above the lateral eyes. Two prominent lenses compose the whole thickness of the test. The lenses are more strongly convex than in *Tretaspis*. In some species of *Phacops* the number of lenses in the lateral eyes are very reduced. In *Phacops pentops* down to 5. Amongst recent Isopoda the number in some cases is reduced to only one lens. This caused Richter to consider the two-lensed eye of *Harpes* homologous to the usual lateral eyes of Trilobites. On account of the close resemblance of Harpes and *Tretaspis* I come to the conclusion that the lateral tubercles found in the family Trinucleidae represent true lateral eyes where the number of lenses is reduced to one.

The marginal suture.

The marginal suture is found in all better known Trinucleidae. The suture is more or less visible on the marginal band. In some cases a raised line is found, in others a fine dark line or fissure. Pl. 11, Fig. 12 shows the suture in *Tretaspis kiæri.* The upper lamella of fringe is easy to split off along this line in the preserved specimens. In some species, as *Tretaspis seticornis,* the lower lamella is lacking in a number of preserved specimens. It is always broken off along the marginal suture. In Pl. 11, Fig. 4 a—c the lamella is partly broken off. In this species about one half of the present specimens lack lower lamella. In the allied species *Tretaspis kiæri* only a few are found without the lower lamella. The specimens with both lamellae certainly represent dead animals, but the others are perhaps only the sloughs from the moulting.

The structure of the marginal suture has been studied in a number of sections. It is usually well marked as a dark line crossing the shell. (Pl. 13, Fig. 8, Pl. 14, Fig. 3). The suture line is also visible crossing the hollow pillars. Oehlert (1895 Fig. k, 1) recognised this line, but gave another explanation of it, as will be discussed on p. 102. Richter (1921 b) has given a careful description of the marginal suture in *Harpes,* (p. 215). He says: "Eine Nacht am Rande des Kopfschildes ist sehr ausgeprägt." The marginal suture of *Trinucleus* has been discussed by several authors. It has often been regarded as not being a real suture. Warburg (1925, p. 45) studied the marginal suture in *Tretaspis seticornis* from Sweden. She says about the specimens from Dalarne of *T. seticornis* "in them there does not seem to be an open suture, but along the same line as where the suture is seen in *Tr. concentricus* Eaton [*Cryptolithus tesselatus* Green] and *Tr. [Cryptolithus] Bureaui* Oehl. according to Reed (1912 a p. 347) and Oehlert (1895 p. 317) there is only a very thin outer layer of the test, the inner part of which is pierced by a fissure". This is not proved by the present investigations. The sections show no thinning of the shell. but a marked split line.

All the slices examined from different species of the Trinucleidae have a well marked marginal suture. A fusion of the shell along the suture line has not been found. The marginal suture in the Trinucleidae seems to have the same structure as in *Harpes.*

The question of the relationship between the facial and marginal suture has been the subject of several discussions in works on trilobites. Reed (1916 p. 170) discusses the lack of facial suture in the Trinucleidae. In the earliest Trinucleidae, *Trinucleus murchisoni, T. gibbsi* and *T. etheridgei* "an oblique ridge or line of bending" is found in the anterior portion, of the cheek lobes. Reed states p. 171: "this ridge has the course of the true facial skture in members of the opisthoparia, and may possibly be regarded as marking the line of fusion between the free and fixed cheeks".

The present material of *Trinucleus* and *Reedolithus* makes it little probable that the bending line should represent a fused suture. The larval stages of those genera and *Tretaspis* (Pl. 7) show no traces of the suture in that place. The line probably only bounds the reticulated posterior portion of the cheek lobe from the steep, smooth anterior portion. In the Meraspid and adult stages of the Trinucleidae no traces of the facial suture is found. In the earliest Meraspid stage the marginal suture and the lateral eye tubercle are quite separated. Pl. 8, Fig. 3 a indicates that the marginal suture has perhaps not been marginal in the Protaspid stage.

The connection between the marginal and facial suture cannot be decided with our present knowlegde.

Muscular Impressions in the Shell of Trinucleidae.

Well preserved specimens of Trinucleidae often show particular structures of the shell. The rather light coloured surface of the shell is interrupted by dark spots or fields of a distinct arrangement. These features have been found within species of *Trinucleus*, *Reedolithus* and *Tretaspis*. Pl. 5, Fig. 4 shows the darker spots on the glabella corresponding to the glabellar furrows. The inner surface of these spots has specially been studied in *Tretaspis*. The small granulae occurring on the surface are lacking beneath the spots. The spots appear quite smooth, and are thus well distinguished from the surrounding shell. The black spots are found on thorax and pygidium. Pl. 10, Fig. 4 illustrates the inner cast of the pygidium of *Tretaspis kiæri*. The black spots are drawn in Fig. 38. In sections the spots are to a certain degree different to the rest of the shell. They appear faint brownish coloured.

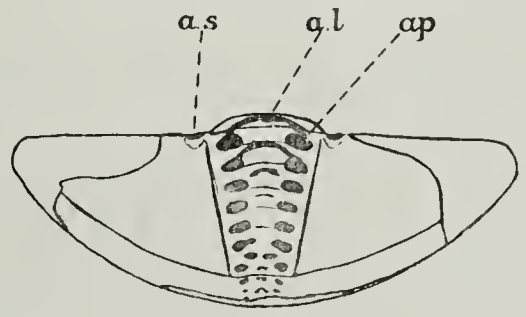


Fig. 38. *Tretaspis kiæri* n. sp. × 1.5. Pygidium with muscular impressions, appendifies, on *ap* = appendifies. *al* = atachment of liegement. *as* = articulating sochet. (The specimen figured Pl. 10, Fig. 40).

Arrangement of the spots.

The well preserved specimen of *Trinucleus foveolatus* var. *intermedius*, Pl. 1, Fig. 1—3, has a darker colour at certain places of the cephalon. In Fig. 39 the dark spots or field are hatched. The dark fields are found in: (1) the glabellar furrows, (2) partly on the ridges from median tubercle of glabella, (3) the axial furrows with the antennuary pits, (4) the frontal furrow, (5) within the radial sulci of the fringe, (6) the lateral eye tubercles, (7) the occipital segment.

On the thorax the dark spots are found within the deep pits in the articulating furrow of rachis. The material of pygidae has been more useful

for the determination of the arrangement of the spots. The segments of the pygidium are easily compared with those of the thorax. Fig. 38 indicates the arrangement of dark spots. Very distinct black spots are found in the lateral portion of the articulating ring. 10 pairs of spots are present. In the front of each segment a narrow arched dark line is visible. Near the posterior band the arrangement is somewhat different to that in front. Three pairs of spots are seen on the posterior band.

Explanation of the spots.

Walcott (1921) among others regards the deep pits on thorax as processes for muscular attachment. They are called appendifers. The name will be used in this paper. They appear on the inside of the shell as distinct elevated processes. Pl. 14, Fig. 5 gives a good illustration of the deep pits. The thin shell at the top of the processes is a little darker of colour than the rest of the shell. The same processes are found on the pygidium and the occipital segment. On the appendifers Walcott assumes an attachment of muscles from the extremities atached to the lower membran. The glabellar furrows must be similar muscular attachments. Holmgren (1916) points out, however, that the anterior segments of *Limulus* are not well marked on the dorsal side of specimens belonging to this genus. He finds no lobes or rings corresponding to the anterior segments. He says (p. 87): "Aber von 2—3 (Augen + antennal segments mit Extrem.; Chelicere segment) sollte man erwarten können dass es auf der Dorsalseite wenigsten angedeutet wäre, denn die Cheliceren und Pedipalpen sind ja Extremiteten, welche nicht als rud. betrachten werden können." Holmgren does not mention the muscular impressions on the dorsal side of *Limulus*. Patten (1912 p. 247, Fig. 155) figures the muscular impressions of the ventral extremities. The impressions are very similar and may be compared with those in trilobites.

In the Trinucleidae we find 3 pairs of glabellar furrows without the lateral pit in the occipital furrow. These furrows are, as above mentioned often indicated by a darker colour similar to that found in the appendifers. In the axial furrow the deep antennuary pits are found. They were first described by Oehlert (1895 p. 302) who considered them to be openings of the antennae. This caused Reed (1914 p. 351) to propose the name "pseudo-antennuary pits". The pits have the same morphological characters as the appendifers on thorax and pygidium and lie in a straight line with the glabellar furrows. Raymond has restorted the lower side of *Cryptolithus tesselatus* (1920 Fig. 20). The Fig. 38 copied from Raymond compares the lower side of *C. tesselatus* with the upper side of *Trinucleus foveolatus* var. *intermedius*. The basis of the 5 appendages quite corresponds to the antennuary pits, the 3 pairs of glabellar furrows, and the pair of lateral pits in the occipital furrow. It is highly probable that the antennuary

pits are identical with the muscular attachment of the antennae. This has been my reason for using the old name antennuary pits instead of pseudo-antennuary pits. In the restored figure of *Cryptolithus tesselatus* (Raymond 1920 Fig. 20) the basis of the appendages does not quite agree with the position of the 4 glabellar furrows. The appendages are situated a little too far posteriorly. This might perhaps be due to the material which is not very complete. The appendifers probably not only represent the atachments of muscles from the appendages, but also other kinds of muscles which will not be discussed in the present paper.

The above mentioned considerations make it probable that the antennuary pits in the Trinucleidae are homologous with the first of four pairs of glabellar furrows found in several trilobites.

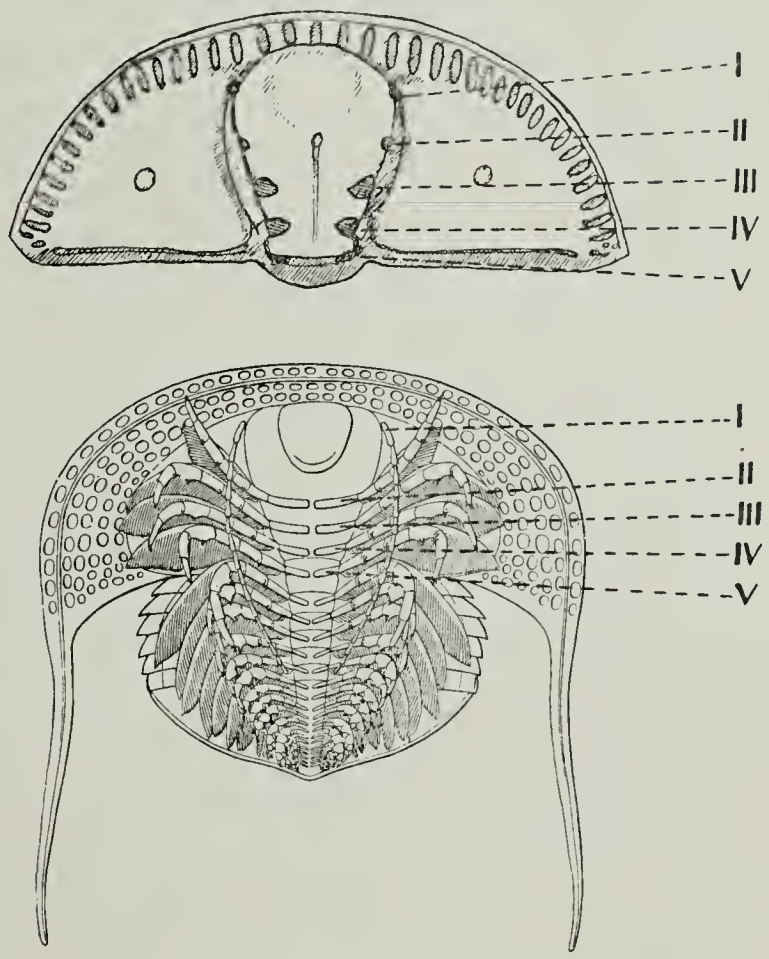


Fig. 39. The correspondance of the glabellar furrows and the appendages on the lower side. Above: *Trinucleus foveolatus* Ang. var. *intermedius* n. var. from Ogygia shale Asker (H 391 Pal. Mus. Oslo). Below: *Cryptolithus tesselatus* (Green). Reproduced after Raymond (1920, Fig. 20).

The segmentation of the head of the trilobites has been the subject of several investigations and discussions. Raymond (1920) mentions the various earlier authors; later Warburg (1925) and Henriksen (1926) have written on the same subject. All the authors seem to have separated the different segments of the glabella by the glabellar furrows. In the larval stage of the Cambrian trilobites the glabella is divided by transverse furrows in segmental rings. At later stages the transverse furrows become glabellar furrows.

In the family Trinucleidae the earlier larval stages show no glabellar furrows. The glabella is not divided in a number of segments. The glabellar furrows are developed in the later stages. As above discussed the glabellar furrows represent the attachments of the muscles of the appendages of the cephalon. On the thorax, where the different segments are free, the attachment of the muscles of the appendages, lie in the anterior portion of the segment. The attachments, the appendifers do not form an anterior boundary of the segment, they lie within the segment. Returning to the glabellar furrows, we must regard them as lying within the segments of the cephalon. They do not form a boundary between each segment as is usually assumed.

The posterior pairs of glabellar furrows are strongly developed in some genera of Trinucleidae. It is probably due to a strong development of the mandibulae and the maxillae.

The position of the antennuary pits and glabellar furrows does not give any facts to solve the question whether the antennulae or the antennae are reduced in the trilobites.

The dark fields in the sulci, in the axial and the frontal furrows and around the eyes, probably represent different kinds of ligament attachment.

Impressions on the inner cast of the glabella have been explained in different ways. The impressions are well preserved in *Trinucleus bucculentus* p. 22 and *Tretaspis seticornis* p. 56 and Fig. 40. Ruedemann (1916 b) described similar shapes in *Cryptolithus tesselatus*.

He found a little nodule just in front of median tubercle. This is not found in *Trinucleus* and *Tretaspis*. He explained the ridges (fissures) as rudiments of a facial suture. I think it more probable to compare the features as indicated by Richter (1923 p. 79) with the glabellar impressions found in *Chasmops*. The impressions are explained by Richter (1923 p. 84): "Die Eindrücke an Glatzenstirn und Hypostom waren die Ansätze von Muskeln. Diese Muskeln waren die Erweitern des Vormagens". It is also possible to connect the fissures with the median eye.

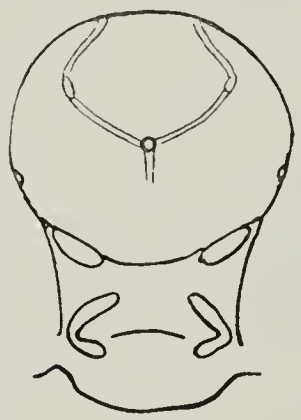


Fig. 40. *Tretaspis seticornis* (His.). Impresssions on the glabella.

On the thorax there are besides the appendifers some other impressions or dark fields. Pl. 14, Fig. 5 shows a darker coloured fissure or pit in the low surface of the axial ring. It probably represents muscular attachment. The kind of muscles are not decided.

In the pygidium dark lines and spots are found between the appendifers, in front of each segment. These surely also represent muscular attachments, probably extensor or adductor muscles. The muscular arrangement of trilobites is discussed by Raymond (1920 p. 91).

Shell structures of the Trinucleidae.

Examining the literature on trilobites I have found very little concerning the shell structure, Lorentz (1906 p. 69) founded a classification of Cambrian trilobites partly on the shell structure. He mentions two different groups having perforated and compact shells. No further description of the structure of the shell is given. Reed (1916 p. 122) indicates two layers in the shell of *Trinucleus* on account of the very variable structure of the surface of the shell of one species. My investigations show great variation in the reticulation of the shell-surface. The two layers of

Reed are not found in the section, and probably are due to individual variations and a less good preservation.

The Norwegian material of Trinucleidae gives good conditions for shell investigations. About 80 sections have been made of different species from several localities. Good sections have only been found among the genera *Trinucleus* and *Tretaspis*. For comparison some slides of Baltic Asaphidae have been made. They seem, in spite of their good preservation, not to give good details of shell structure. A dyeing of the sections with $FeCl_3 + K_4Fe(Cn)_6$ has been tried without success.

The preserved shell of Trinucleidae usually consists of calcite. Sometimes quartz is found among the calcite. A very successful preservation of the shell is found in the Trinucleus shales and limestone at Ringerike, Norway. To the matrix of calcite with quartz small quantities of pyrite is added. In some cases the shell is quite filled with pyrite. All transitions in the quantities of pyrite are found. As is discussed below the small grains of pyrite in some cases are found in a distinct arrangement indicating the primary structure of the shell. The pyrite incrustation has served as a perfect dyeing method comparable with the well known Golgi method. In most cases the grains of pyrite are too large to show the minute structure.

The well preserved specimens of *Tretaspis kiæri* show some details of the shell structure. The outer layer of the shell (see Pl. 13, Fig. 3) has a brown colour. The outer limit is usually badly preserved. In some cases the inner layers of the shell show a yellow colour indicating a difference from the larger white layer in the middle.

The pyrite-incrusted specimens of *Tretaspis seticornis* show several details of the structure. Pl. 12, Fig. 1—5 illustrate the preservation. The specimen on Pl. 12, Fig. 1 has a distinct brown coloured outer layer of the shell (pg. l). The thickness of this layer diminishes somewhat just beneath the reticulate list of the glabella. In some sections the outer limit against the surface is indicated by a darker line (o.l? on Pl. 12, Fig. 4), which differs from the lighter hue of the layer. The brownish-yellow layer is only slightly encrusted with pyrites.

Beneath the brown outer layer a white layer strongly encrusted with pyrite is visible (pr.l on Pl. 12, Fig. 1). The outer limit is usually very distinct. The inner limit is more or less marked. This layer represents more than $^2/_3$ of the thickness of the shell.

The characteristic feature of this layer is the numerous grains of pyrite radially and concentrically arranged (Pl. 12, Fig, 1—5). In Pl. 12, Fig. 2—4 the radial arrangement of the grains is very distinct. The very small grains of pyrite are arranged in straight lines. Seen with a stereoscopic ocular the lines of grains lie in different layers of the section. This may also be studied with the micrometric screw. In some cases cracks are filled with pyrite grains. They are easily separable from the radial lines of

grains. The size of the grains in the radial lines varies. In some cases they are very minute and scarcely visible in the photograph (Pl. 10, Fig. 4). The fine lines of pyrite grains are usually disturbed and replaced by larger grains which often fill the main part of the layer.

In some few specimens distinct laminated structure of the layer has been determined. Pl. 10, Fig. 4,5 show such an arrangement of the pyrite grains. The radial lines are also present. The concentric lines of grains go through the total thickness of the section. This indicates an arrangement in spaces which shows the laminated structure of the layer. 7—8 layers with about the same distance are easily distinguishable. A closer study shows several less marked layers with a very small distance among the others.

In polarized light the thick layer above described shows faint traces of extinguision.

The inner layer usually shows no distinct limitation to the median layer (in. 1 on Pl. 12, Fig. 1, 4). The inner layer has a white or yellow colour. Radial lines of pyrite grains are not common and only found in the outer part near the median layer. The thickness somewhat larger than in the outer layer.

In polarized light this layer extinguishes very distinctly. That indicates a determined arrangement of calcite.

In *Trinucleus bronni.* (Pl. 13, Fig. 8) traces of the 3 layers are visible. The inner layer is seen within the fringe.

In order to explain the structures found, the literature of shell structures of recent arthropoda has been studied.

Biedermann (1914) gives a review of the investigations on the crustacean shell. Bütschli (1898) has discussed the earlier results. 4 layers of the shell are separable.

1. A thin outer layer, aussenlage (Bütschli), cuticula (V. Izon), epidermis (V. Nathusius, Lavalle), pellicula (Williamson), of about 7 η.

2. The pigment layer, pigmentlage (Lavalle, Vitzon, Bütschli), cellular layer (Carpenter, Queckett), areolated layer (Williamson), Wabenschickt (Nathusius).

3. The principle layer, hauptlage (Bütschli), couche dermique (Lavalle), corium calcified (Williamson), mittlere panzerschickt (Nathusius), innere schickt (Tullberg), couche calcifi (V. Izon). The principle layer forms the chief part of the thickness of the shell.

4. The inner layer, innenlage, has usually not been separated from the principle layer. Williamson, Tullberg and Bütschli have mentioned it. Bütschli (1898) states that it shows no distinct limit to the overlying principle layer. Besides the above mentioned 4 layers Bütschli mentions a very thin (about 1 η thick) "grenz kant" above the outer layer.

The 3 thicker layers (2—4) show fine tubulae or canaliculae (Porkanälchen). According to Tullberg (1882, p. 8) the inner layer in *Homarus* shows nearly no traces of radial tubulae.

Bütschli (1908) (see Biedermann, 1914, p. 847) has found very little double refraction in the pigment layer of decalcified shells of crustacea. The upper part of the principle layer and the inner layer show rather strong double refraction. The lower part of the principle layer has a very faint double refraction. Biedermann (1914) has found a distinct lamination of the shell showing opposite extinguision.

Comparing the shell structures of recent arthropoda, specially crustacea, with those of *Tretaspis* we find a striking resemblance.

Fig. 41 shows the different layers of the shell of *Homarus* (after Tullberg) compared with those found in *Tretaspis*.

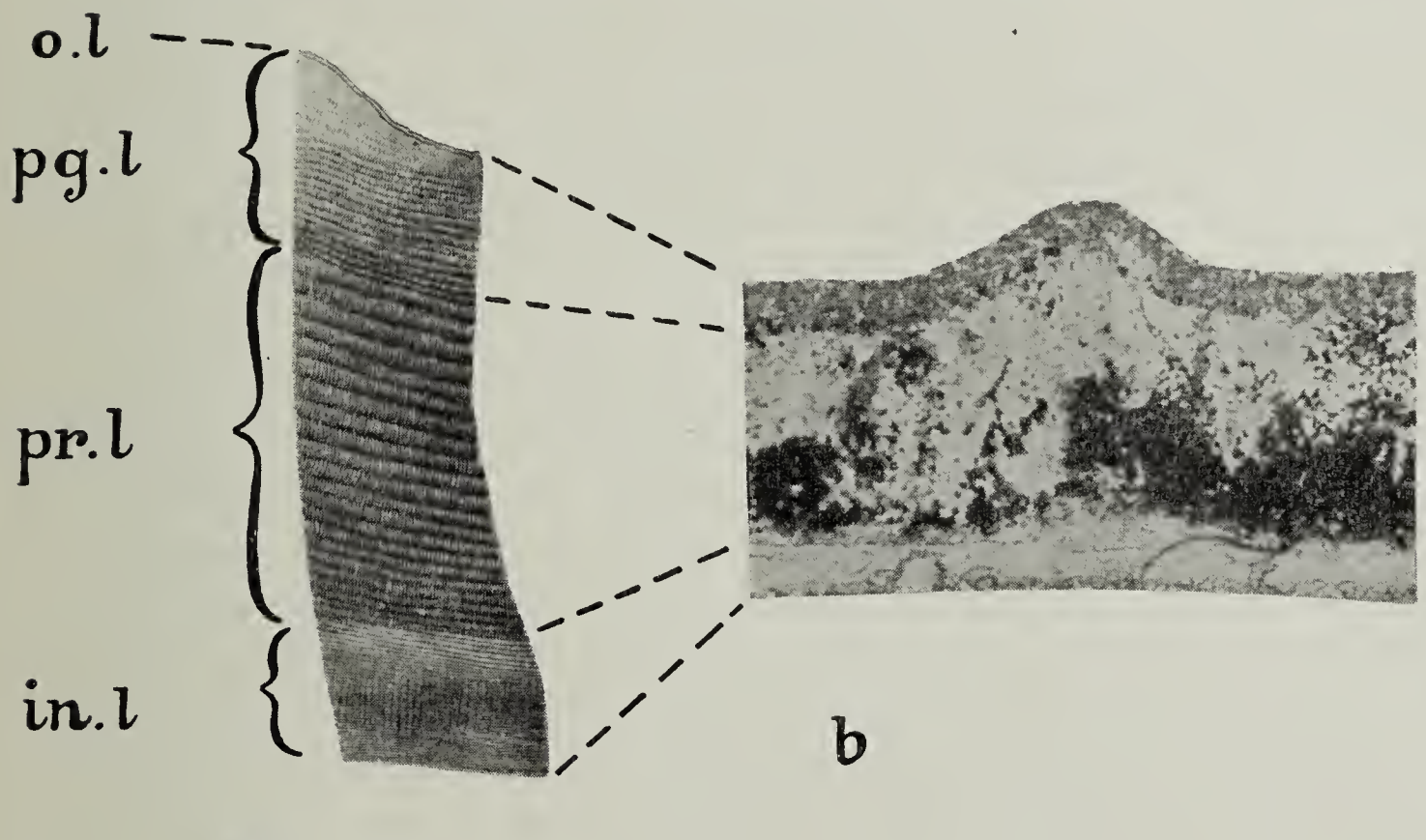


Fig. 41. Shell structures of *Homarus* and *Tretaspis*. *a* = reproduced from Tullberg (1882). *b* = Pl. 12 fig. 1. *o.l* = outer layer. *pg.l* = pigment layer. *pr.l* = principle layer. *in.l* = inner layer.

1. The outer layer is not traced with certainty in Trinucleus. A dark outer line suggests the presence of it (o.l.? on Pl. 12, Fig. 4).

2. The brown-coloured outer layer fully agrees with the pigment layer. The lack of extinguision is common to both.

3. The median layer has the same thickness as the principle layer. The laminated structure is also most prominent in this layer. The extinguision of the minute lamellae is not found, but this is probably due to the preservation.

4. The inner layer is not clearly limited from the principle layer. It closely resembles the inner layer, and shows as this a distinct extinguision.

5. The minute tubulae or canaliculae are found also in the Trinucleidae. They are most common in the principle layer, but also occur in the outer and inner layers.

As a conclusion we may state that the shell structure of the *Trinucleidae* fully corresponds to that of the recent arthropoda.

PATTEN (1912 p. 297) has figured a section of the shell of *Limulus*. I have not been able to find a detailed description of the different layers of the shell in *Limulus*. It cannot be decided if the *Limulus* or crustacean shell is most allied to the trilobite shell.

Marginal Canals in the Shell of the Trinucleidae.

LOVÉN's figure of *Tretaspis seticornis* from Dalarne shows many fine details (1844, Pl. 2, Fig. 1 *b*). On the margin of the fringe several small black spots are drawn (fig. 42).

I have had the opportunity of examining a large number of these specimens from the Trinucleus shales at Dalarne in Sweden. I was soon aware of the minute punctuate structure of the fringe. It is found only in some adult specimens. The younger ones show no distinct spots.

Description of the structure. On the white shell some minute black spots are visible. The diameter of the spots is about 0,03 mms. The spots are found on the fringe and the posterio-lateral parts of the cheek lobes. They are numerous on the margin of the fringe. (Pl. 11, Fig. 4 *a*—*c*). On the marginal band just above and below the marginal suture the number is a little smaller than on the arched surfaces of the rims. Only a few spots are seen on the fringe. On the cheek lobes the number diminishes rapidly. The top of the cheek lobes seems to be without the black spots. The material which I have borrowed from Sweden is regrettably too scarce to give the distinct distribution.

The single pits show some variation. Pl. 11, Fig. 4 *a*—*c*, show the spots on the margin of the fringe. On the margin where number of pits are great, the pits to a certain degree appear as very small elevations with a flat black spot on the top. On the marginal band the spots occur as small round pits. The same is found on the arched surface of the ventral rim, where the pits are found between the developed terrace lines.

The black colour of the spots indicates openings in the white shell filled with the black matrix of the surrounding shale. The single possibility that the spots on the margin should have been pustules broken off is not probable. The shell is too thick and the pits on the ventral rim show true impressions.

It has not been possible to get good sections of the Dalarne specimens.

The Norwegian material has been examined to find the mentioned openings. These have been found on the fringe of *Tretaspis seticornis*, *T. cerioides* and *T. kiæri*. The white shell in a black shale is not found in Norway. The beautifully preserved limestone specimens show the openings very distinctly in some cases. Pl. 11, Fig. 12, shows the openings in *T. kiæri*.

The pits are especially distinct above the marginal suture. *T. cerioides* shows partially small elevations instead of pits on the upper fringe. These certainly are the same openings (H 385). In *T. seticornis* the openings are visible in a number of specimens but they are difficult to distinguish from the surrounding shell of the same colour.

Fig. 42. *Tretaspis seticornis* (His.) (after Lovén 1845). Lateral portion of fringe showing pits and small canal openings.

The small openings on the fringe seem to be a distinct feature among the *Tretaspis* species and occur probably also among other genera and families.

As above mentioned these structures must be explained as openings in the shell. From this point of view I have examined a number of sections of Trinucleidae to find possible canals in the shell. Practically no section showed any traces of such canals.

Canals in the relatively thick sections may be traced with the micrometric screw or a stereoscopic ocular. The stay lines from the terrace lines show no canal character. The FeS_2-stained specimens of *Tretaspis seticornis* give no certain traces of the canals. Distinct canals are found in *Trinucleus bronni*. Pl. 13, Fig. 8 gives a photo of a transverse section of the fringe. The shell is penetrated by several pillar-shaped structures. Through the thickness of the section the pillars are found in different layers. Each pillar consists of numerous fine grains of probably FeS_2, which are distributed in pillars of a slight hour-glass structure. The structure and distribution are indicated in Fig. 43. The structure and arrangement of the pillars completely agree with the openings found on the shell surface of different *Tretaspis* species. The original canals must have been impregnated with FeS_2.

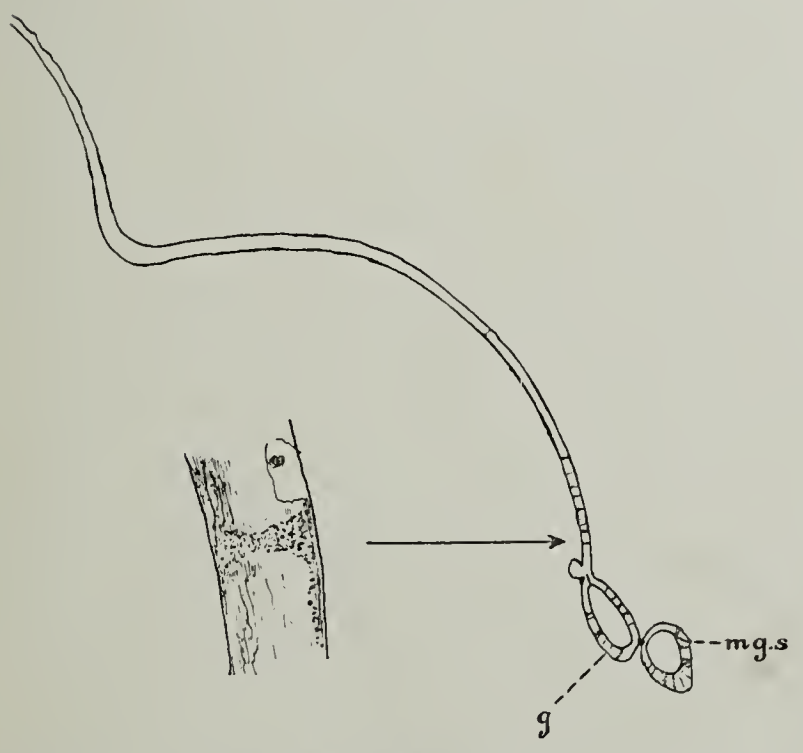


Fig. 43. *Trinucleus bronni* (Sars et Boeck). × 12 and × 120. Section of fringe and cheek lobe. Canals visible on fringe and lateral part of cheek lobe. (Comp. Pl. 13, fig. 8).

The facts show that the marginal portion of the cephalon of the Trinucleidae was pierced by numerous fine canals. The canals are most common in the most exposed parts of the cephalon, ɔ: on the marginal rims.

Openings of canals in the shell are very common among the recent arthropoda. Patten describes several cutaneous sense organs in *Limulus*. (1912 p. 110).

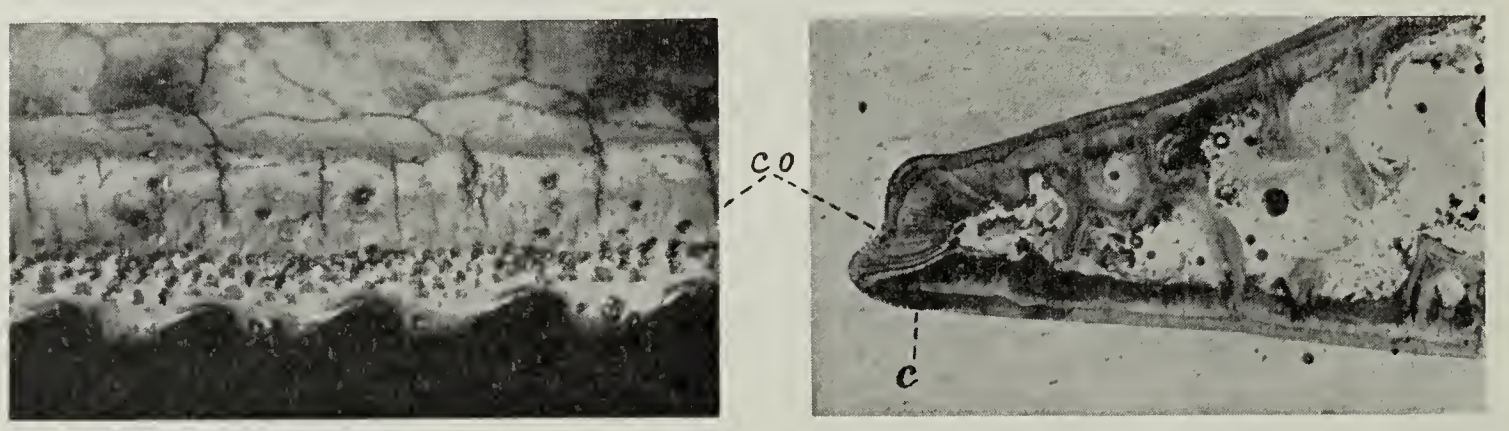


Fig. 44. Marginal portion of the cephalon of adult *Limulus*. $a \times 9$, $b \times 6{,}4$. a = lateral view, b = section. *co* = canal openings. *c* = canals.

The most sensitive areas are the margins of carapace (p. 111).

Fig. 44 shows the margin of an adult *Limulus*. The canal openings are seen. We find the greatest number at the margin as in trilobites. The section of the fringe shows the canals. Sections of the small branchipoda as *Apus* have not been made.

The structure of the hollow pillars in the Fringe.

A number of authors have discussed the subject. A more detailed study has been carried out by Oehlert (1895) and Richter (1921 b). The latter has studied the structures in the genus *Harpes*.

Reed (1912) has carried out the arrangement of pits (hollow pillars) on the upper and lower lamella of fringe on a great number of the known Trinucleidae. He found that the pits on the upper lamella in some species of *Trinucleus*, not always correspond to those on the lower lamella. The detailed study of the fringe of Norwegian Trinucleus has shown that the pits on both lamellae always correspond and are connected by hollow pillars. It seems probable that a bad preservation has disturbed the correspondence of the pits on the two lamellae of the British species. The variation of pits within a species may also give rise to the assumption of a difference in pits on the two lamellae. The assumption of "blind pits" agrees with the hypothesis suggested by Oehlert (1895) by which the pits are developed from each lamella. In his careful studies Oehlert found the marginal suture line, but it was explained as a coalescence line. The nonperforated structure of the pillars seems very probable after having examined some sections. The general shape of the pits in *Tretaspis* is illustrated in Fig. 45. It has usually been described as conical, but the median part is steep and the bottom is strongly flattened.

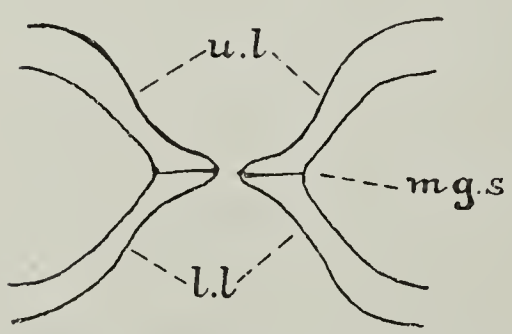


Fig. 45. Diagram of hollow pillars in *Tretaspis*. *u.l* = upper lamella. *l.l* = lower lamella. *mg.s* = marginal suture.

On the well preserved specimen Pl. 11 Fig. 10 the small opening in the middle of the bottom of the pits is seen. Sections of the pits do not generally cross the small openings, and the pits appear to be non-perforated.

The present material shows, what has also been assumed by several earlier authors, that the fringe is perforated.

Richter (1921 *b*, p. 188) has discussed the structure and origin of the hollow pillars. He finds similar shapes in the recent cassiidae. The origin of the pillars is explained (p. 190): "So abenteuerlich ihre Gestaltung, ist die Siebhaube nur die Auswirking einer bei Arthropoden allgemein verbreiteten Anlage, der zelligen Querstränge." He does not mention the interesting staying structures of the old specimens of *Limulus* (Patten 1912 p. 296). They are found in the lateral area and round the eyes. The structures are visible in Fig. 44 *b*.

Terrace lines in the Trinucleidae.

The terrace lines are well known in Trilobites. They consist of raised lines more or less parallelly arranged. Richter (1923) has discussed the structure. He mentions 2 sets of lines at right angles to each other. He explains it as a "corrugated plate structure" which serves to strengthen the flat surface of the shell. It is e. g. common amongst the Asaphidae.

Among the Trinucleidae terrace lines are found at several places of the shell. On the cephalon they occur on the fringe especially on the girder and below the marginal suture. On the pygidium terrace lines are found on the posterior band.

As the outer surface of the fringe is usually not preserved, the structure has been studied in rather few specimens. The terrace lines on the fringe might be studied on: *Reedolithus carinatus*, Pl. 5, Fig. 18, *Tretaspis seticornis*, Pl. 8, Fig. 6 and Pl. 11, Fig. 4 *b—c*, *T. cerioides* var. *angelini*, Pl. 9, Fig. 7, *T. latilimbus*, Pl. 11, Fig. 11.

The sections show the inner structure of the terrace lines. Lindstrøm (1901, Pl. 1, Fig. 15) and Richter (1921 b Pl. 17, Fig. 12—13), figure sections of the terrace lines on *Asaphus* and *Harpes*.

They do not give any further description of the structure.

On Pl. 14, Fig. 1, 3, 4, the structure of the terrace lines in *Tretaspis kiaeri* and *T. seticornis* are seen. From the raised lines (terrace lines) on the girder dark radial lines are seen in the shell. Highly magnified the lines show no distinct thickness. They do not occur as canals but continue through the thickness of the sections. They must be regarded as structural limit lines in the shell. In polarized light the extinction is uneven on the different sides of the lines.

I agree with Richter's (1923) assumption of the terrace lines as streng thening lines.

On the glabella similar structures are found in the shell. *Tretaspis kiaeri* with its highly reticulated surface of glabella shows distinct dark lines in the shell. They are radially arranged near the surface, but bend round near the inner layer of the shell. (Pl. 14, Fig. 1, 2) (Pl. 13, Fig. 3). These lines are always found from the centre of the reticulating lists. In *Tretaspis seticornis* with its faint reticulation the same is found. (Pl. 13, Fig. 7).

Compared with the structure of the terrace lines the structure of the reticulating lists shows a great resemblance. We must assume the reticulating list and the terrace lines to be homologous formations. The glabellar reticulation in *Trinucleus bucculentus* shows great resemblance to the terrace lines (Pl. 2, Fig. 8—10). The lists have a concentric arrangement with the median tubercle as a centre.

Trinucleus foveolatus (Pl. 1, Fig. 4, 13) shows a transition to the high reticulated species as *Tretaspis cerioides* etc. (Pl. 9, Fig. 3).

The concentric lists, found on the upper lamella of fringe of *Tretaspis*, probably also correspond to the terrace lines. Their structure is shown in Pl. 14, Fig. 1. They probably serve to strengthen the fringe.

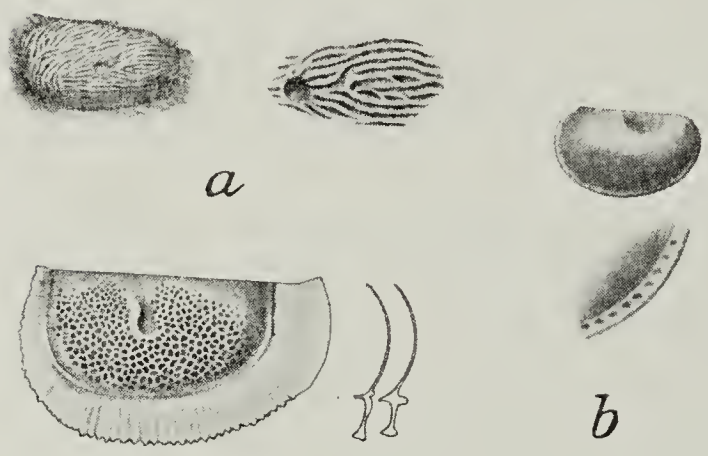


Fig. 46. Palaeozoic Ostracoda with shell surfaces resembling those found in the family Trinucleidae. *a* = *Kirkbya? Walcotti,* Jones. × 15 and × 30. *b* = *Isochilina Ottava,* Jones, var. *intermedia* Jones × 2,5 and × 12,5. Right valve with portion of lateral brim. *c* = *Eurychilina reticulata* Ulrich × 9. Right valve with sections.
a—*b* after Jones (1891, Pl. 10—11). *c* after Ulrich (1889 Pl. 9).

After having described the hollow pillars and the terrace lines the functions of those structures will be discussed. As above mentioned the structures surely serve to strengthen the shell of the trilobite. The "corrugated plate structure" was found by Richter (1923) to be very common in the Trilobite shells.

The strongly convex cephalon of the Trinucleidae with the broad perforate fringe shows very interesting structures concerning the strengthening of the shell.

A number of species show highly reticulated surface of the strongly arched glabella and cheek lobes. The lists make the shell thin and strong. Similar structures are known from recent ostracoda.

On the fringe the above mentioned corrugated structure is represented by the radial sulci and the beams lying between them on the upper and lower lamella. The sulci are always found on the concave surface of the lamellae. In *Tretaspis* they are found between the brim and cheek-roll on the upper lamella and on the inner band on the lower lamella. The concave upper lamella of *Trinucleus* has distinct radial sulci. The inner band on the lower lamella is flat without sulci. The rather flat

lamella of *Cryptolithus* usually lacks radial sulci on both lamellae. The stay-structures formed by the radial sulci may be compared with the frames in a boat.

Besides the radial strengthening of the fringe a concentric one is also found. It consists of the strong girder and the marginal rims (Kämpferliste und randliste, RICHTER 1921 b, p. 187). The girder is supported in some genera, *Cryptolithus* and *Reedolithus*, by secondary "girders" within the real girder.

The strong girder and marginal rims are stayed by the terrace lines.

On the convex surface of the upper lamella the fringe is stayed by concentric lists.

The concentrically arranged stay lines of the fringe are found on the convex surfaces while the radial lines occur on the concave. The former may be compared with the planks of a boat. The hollow pillars serve to keep the two lamellae of the fringe together and thus further strengthen the fringe.

The structures of the test of the Trinucleidae show highly specialized characters in the direction of making the shell as strong and light as possible.

Some species of ostracoda show structures reminding of those in Trinucleidae.

Fig. 46 *a* illustrates a reticulated surface similar to the glabella and cheek lobes of *Trinucleus foveolatus*. Fig. 46 *b* indicates a narrow fringe with one row of pits. A hollow character of the pits is probably not known. Fig. 46 *c* shows a reticulated surface on the median portion and faint radial sulci on the brim (fringe). The sections of fringe resemble those of Trinucleidae.

Mode of life of the Trinucleidae.

The methods of life have been discussed especially by DOLLO (1910), RICHTER (1919, 1920) and RAYMOND (1920).

RICHTER in his interesting paper: Von Bau und Leben der Trilobiten (1919—20), refuses many of the results obtained by DOLLO and his pupils STAFF and RECK (1911). These and earlier authors have assumed a completely burrowing mode of life for the Trinucleidae. It was chiefly founded on the reduced lateral eyes and the mud-filled alimentary canal found in *Cryptolithus* by BEYRICH (1846). The reduced lateral eyes are not a proof of a burrowing habit of life. The connection between light and the development of eyes is often difficult to decide. In the recent (1926—27) Handbuch der Zoologi, BREHM says (p. 460) in the chapter on eopepoda: "Überraschenderweise finden wir weder im Süss-noch im Meerwasser einen Zusammenhang zwischen Organisation und Lichverteilung." The Copepode *Calanus finmarchicus* has lateral eyes in the young larval stage but is

apparently blind in the adult stage. The species is found pelagic in dark to light water layers.

According to the mud-filled alimentary canal I agree with RAYMOND (1920 p. 39) who regards it of little general value. STROMER (1909 p. 282) regards the Trilobites as mud-feeders since no stronger masticatory organs have been found. The strong glabellar furrows found in *Tretaspis* indicate well-developed appendages in the posterior part of the head. The masticatory organs seem to have been well developed.

To get a right impression of the body of *Tretaspis* we will regard *T. seticornis* in the well-preserved Norwegian species. Fig. 47 shows a lateral view of a complete specimen. Thorax with pygidium is bent upwards. This is probably due to a destruction of ligaments during the putrification (POMPECKJI 1892 p. 93).

Fig. 47. *Tretaspis seticornis* (HIS.) × 3. Lateral view of complete specimen. Top of glabella broken off. Trinucleus shale Frognø, Ringerike. (H 51 KIÆR coll. Pal. Mus. Oslo).

The cephalon is resting on the level by the outer band of the marginal fringe and the genal spines. The fringe has usually been regarded as resting on the level with the whole margin as in Harpes. This is not the case. The anterior part is bent up as in several other trilobites and in *Limulus*.

The base of the genal spine is a little elevated from the level. The general appearance of the fringe is very like that of Limulus. In the latter a "girder" is found marking off an outer band. The base of the lateral part of the cephalon is like a sledge.

Thorax and pygidium must in outstreched position have been situated above the level as in *Harpes*. RICHTER (1920 p. 25) assumes that the thorax and pygidium have been bent down with the posterior part on the level. The same is found in *Limulus* and has probably been the case in *Tretaspis*. The prolonged genal areas give good protection in this position of the thorax.

The known appendages in *Cryptolithus* (Fig. 39) indicate a swimming power of the genus.

The shell investigations of the Trinucleidae show specialised staying structures obtaining great strength but with as small a weight as possible. This gives support to the possibility of a swimming power of Trinucleidae.

Some species, as *Trinucleus bucculentus*, have a thick, probably heavy shell. According to RICHTER (1919 p. 229) the strongly arched Trilobites, as the *Phacops-calymene* type have a well developed musculature and were

good swimmers. In *T. bucculentus* the great pseudo-frontal lobe probably is due to a strong development of the anterior part of the alimentary canal. The deep appendifers on the thorax indicate well developed appendages.

Probably the adult *Trinucleus* and *Tretaspis* partly lived on the bottom like *Limulus* and partly were active swimmers.

The same is the case with the adult *Reedolithus* and probably also *Cryptolithus*.

The young larval stage of the Trinucleidae were swimmers (Raymond 1920 p. 101). He mentions it as a cause of the great distribution of the species. The general shape of the young Meraspid stages with the long genal spines indicates a pelagic habit of life.

In *Reedolithus* the larval characters are maintained nearly up to the adult stage. Fig. 19, 20 and Pl. 5, Fig. 1—7 shows the highly carinate glabella and the flat broad fringe. The occipital spine might be compared with the zoael spine in young decapoda. Holaspid stages probably had a free swimming habit of life. The carinate glabella and the presence of the occipital spine makes it probable that they swam with the ventral side up, as is e. g. known from young specimens of *Limulus* (Patten 1912 p. 27). The broad flat fringe indicates a partly pelagic mode of life. The carinate glabella would serve as a keel. In the adult stage *R. carinatus* is very like *Tretaspis*.

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PLATES

Plate 1.

Trinucleus foveolatus, Ang. var. *intermedius* n. var. Page 18.

Fig. 1. × 6. Holotype. Cephalon. Ogygia shale, Engervik, Asker. No. H 391. Pal. Mus. Oslo.
„ 2. × 6. Anterior view of the same specimen.
„ 3. × 6. Lateral view, showing glabellar furrows.

Trinucleus foveolatus, Ang. Page 16.

„ 4. × 6. Neotype. Cephalon. Ogygia shale, Norway. No. Ar. 2310. Riksmus. Stockholm. G. Holm coll.
„ 5. × 6. Anterior view showing the flat cheek lobes.
„ 6. × 6. Impression of cephalon of a young specimen. Ogygia shale, Huk, Bygdø, Oslo. No. H 492. Pal. Mus. Oslo. Kiær coll.
„ 7. × 6. Pygidium. Ogygia shales, Bygdø, Oslo. No. H 488. Pal. Mus. Oslo. Kiær coll.
„ 8. × 6. Cephalon and pygidium. Impression of cephalon. Ogygia shale, Huk, Bygdø, Oslo. No. H 538. Pal. Mus. Oslo.
„ 9. × 6. Young cephalon and pygidium probably belonging to this species. Glabella carinate. Ogygia shale. Engervik, Asker. No. H 623. Pal. Mus. Oslo. Aut. coll.
„ 10. × 6. Cheek lobe with a portion of glabella. (Gl). Reduced lateral eye tubercle on the reticulated surface of the cheek lobe. Ogygia shale (?) Norway. No. Ar. 2308. Riksmus. Stockholm. G. Holm coll.
„ 11. × 6. Pygidium. Ogygia shale, Huk, Bygdø, Oslo. No. H 490. Pal. Mus. Oslo. Aut. coll.
„ 12. × 9,7. Cheek lobe with fringe in anterio-lateral view. The pits, hollow pillars (h. p.) are visible in the sulci. Ogygia shale, Huk, Bygdo, Oslo. No. H 392. Pal. Mus. Oslo. Holtedahl coll.
„ 13. × 9,7. Glabella and cheek lobe with reticulated surface of shell. Median- and lateral eye tubercle visible (m. e. and l. c.). Ogygia shale, Toten by Mjosen. No. H 533. Pal. Mus. Oslo.

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Plate 2.

Trinucleus bronni (Sars et Boeck). Page 19.

Fig. 1. × 3,6. Nearly complete specimen. Plastiline impression. Upper Ogygia shale Enge vik, Asker. No. 574. Pal. Mus. Oslo. C. Størmer coll.

„ 2. × 3,6. Ventral view of fringe showing Girder (g) and genal spines (g. s.). Upper Ogygia shale, Killingen, Oslo. No. H 419. Pal. Mus. Oslo. Aut. coll.

„ 3. × 3,6. Cephalon with well preserved fringe. Plastiline impression. Ogygia shale, Asker. No. H 566. Pal. Mus. Oslo.

„ 4. × 3,6. Two cephalae. Plastiline impression. Upper Ogygia shale, Killingen, Oslo. No. H 580. Pal. Mus. Oslo. Aut. coll.

„ 5. × 6. Ventral view of fringe. g = girder. Ogygia shale, Gomnæs, Ringerike. Mo. H 401. Aut. coll. Pal. Mus. Oslo.

„ 6. × 6. Cephalon with upper and lower lamella of fringe (u. l. and l. l.). Ogygia shale, Gomnæs, Ringerike. No. H 417. Pal. Mus. Oslo. Aut. coll.

„ 7. × 6. Ventral view of fringe. Only two rows of pits. Ogygia shale, Killingen, Oslo. no. H 418. Pal. Mus. Oslo. Aut. coll.

Trinucleus bucculentus, Ang. Page 21.

„ 8. × 2. Neotyp. Cephalon with shell surface preserved showing reticulating lists. Ogygia shale, Engervik, Asker. No. H 480. Pal. Mus. Oslo. Kiær coll.

„ 9. × 2. Anterior view showing pits on upper and lower lamella of fringe.

„ 10. × 2. Lateral view.

„ 11. × 2. Cephalon. Internal cast. Ogygia shale (?) Norway. No. Ar. 2323. Riksmus. Stockholm. G. Holm coll.

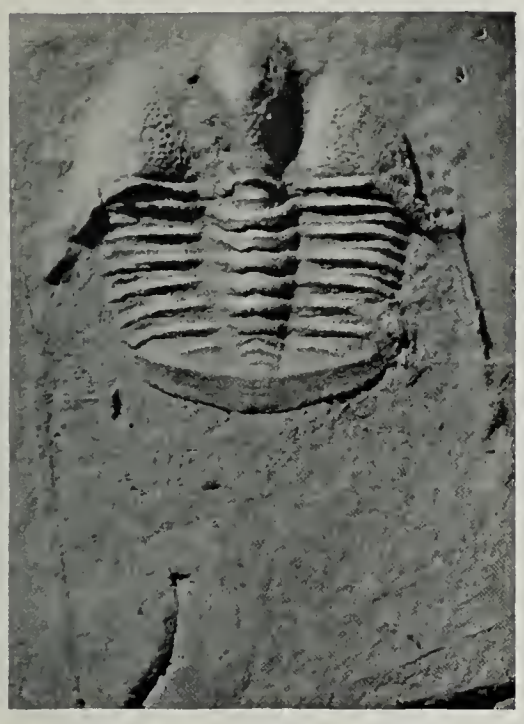
„ 12. × 6. Anterio-lateral view showing characters of fringe. The hollow pillars (h. p.) seen on both lamellae.

„ 13. × 9,7. Internal cast of cheek lobe with small lateral eye tubercle (l. e.) and numerous small granulae. Ogygia shale, Engervik, Asker. No. H 481. Pal. Mus. Oslo. Kiær coll.

„ 14. × 3,5. Enrolled specimen. Posterior thoracic segments and pygidium visible. Ogygia shale, Engervik, Asker. No. H 482. Pal. Mus. Oslo. Kiær coll.

„ 15. × 3,5. The same specimen. Only thorax visible. Deep appendifers (ap.).

„ 16. × 2. Impression of cephalon showing the lower lamella of fringe. g = girder. gl = glabella. Ogygia shale (?) Norway. No. Ar. 2396. Riksmus. Stockholm. G. Holm coll.



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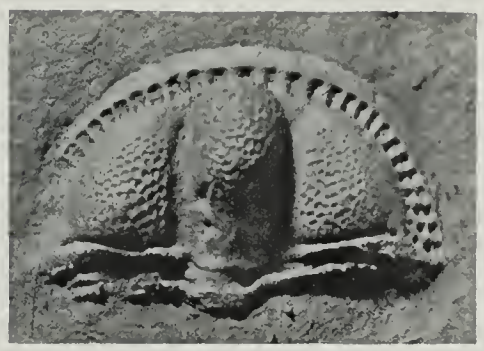

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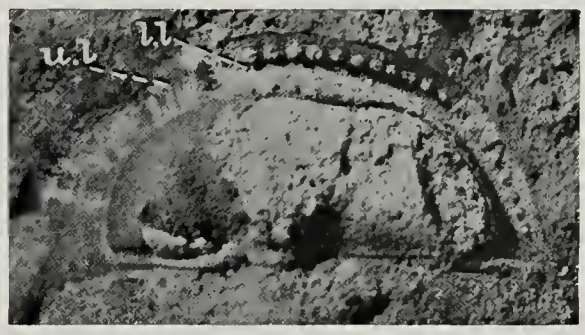

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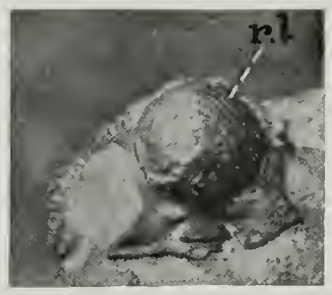

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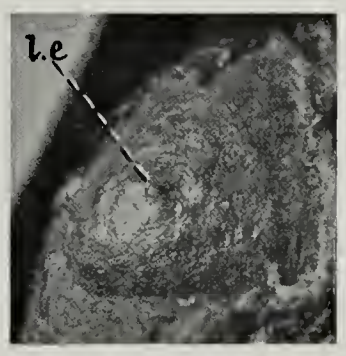

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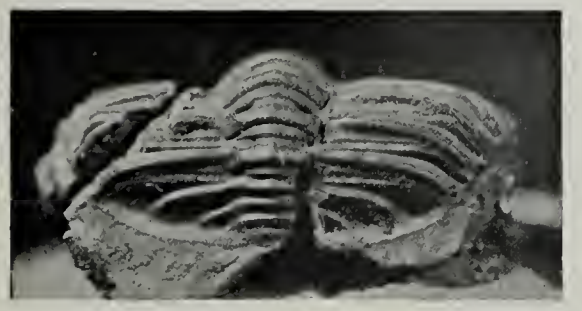

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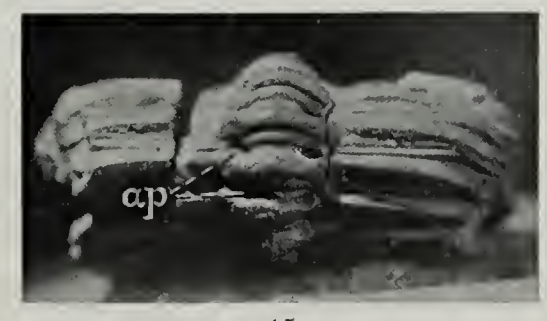

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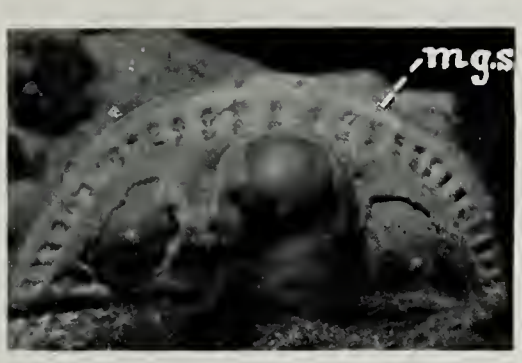
Plate 3.

Trinucleus hibernicus Reed, var *brøggeri* n. var. Page 24.
All specimens from Ampyx limestone, Gullerud, Norderhov, Ringerike.
Pal. Mus. Oslo. Brøgger coll.

Fig. 1. × 6,5. Holotype. Cephalon without shell, but with both lamellae of fringe preserved. Marginal suture (mg. s.) visible. No. H. 553.
„ 2. × 6,5. Cephalon without lower lamella of fringe. No. H 543.
„ 3. × 6,5. Anterior view showing strongly arched cheek lobes.
„ 4. × 6,5. Younger specimen with distinct median eye (m. e.) and lateral eye tubercles. No. H 560.
„ 5. × 6,5. Anterior view.
„ 6. × 6,5. Cephalon with well developed glabellar furrows. No. H 545.
„ 7. × 6,5. Anterior view. Lower lamella of fringe not present..
„ 8. × 11. Prepaired portion of fringe. Posterior view showing lower lamella with girder = (g), hollow pillars or pits (h. p.) very faint on the inner band, but distinct, lying between prominent radial ridges, on the outer. List of integument attachment visible (i. a.). No. H 579.
„ 9. × 11. Ventral view showing the deep radial sulci.
„ 10. × 6,5. Fringe in ventral view. Outer band over lower lamella visible. g = girder, gs = genal spine. No. H 563.
„ 11. × 11. Cheek lobe with reticulated surface of shell. Lateral eye tubercle (l. e.) smooth. No. H 557.
„ 12. × 11. Pygidium. Larval stage. Rachis faintly marked. No. H 558.
„ 13. × 6,5. Pygidium. No. H 549.
„ 14. × 6,5. Lateral portion of cephalon. The shallow radial sulci holding two pits, seen on the fringe. Marginal suture (mg.s.) distinct in the lateral portion. g.s. = genal spine. No. H 544.



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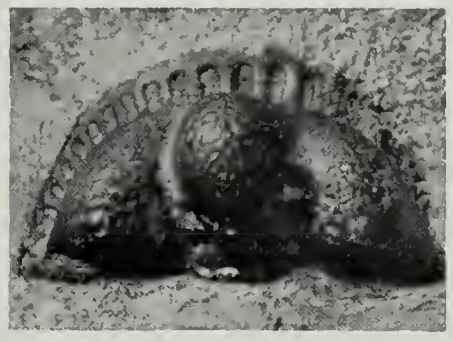

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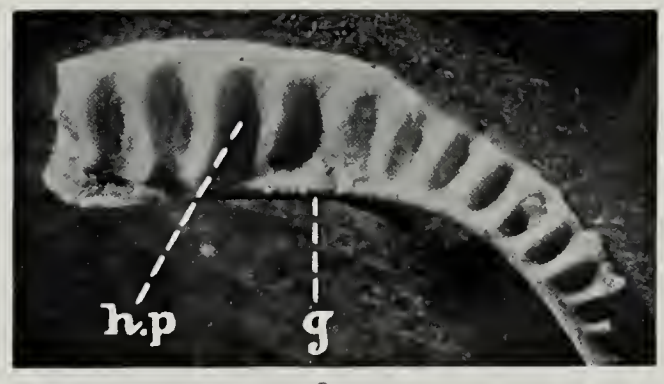

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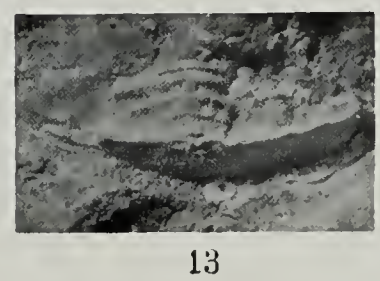

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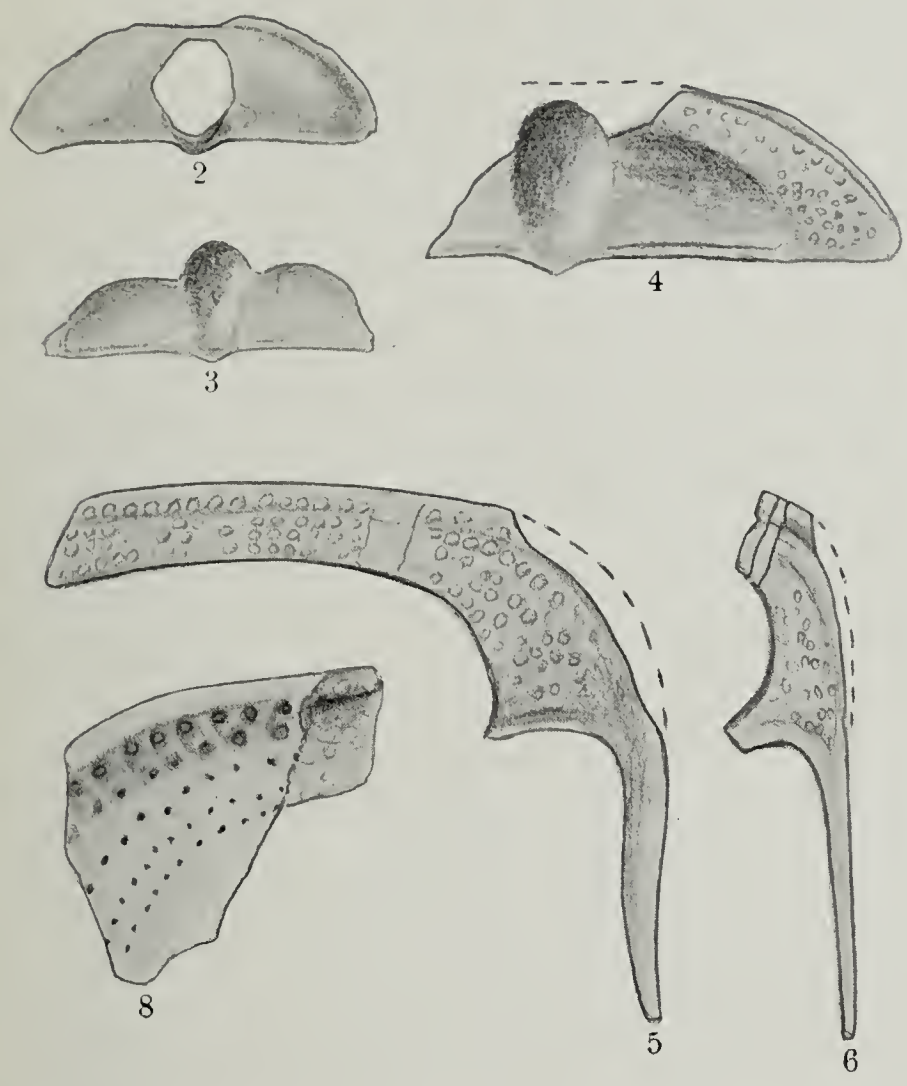
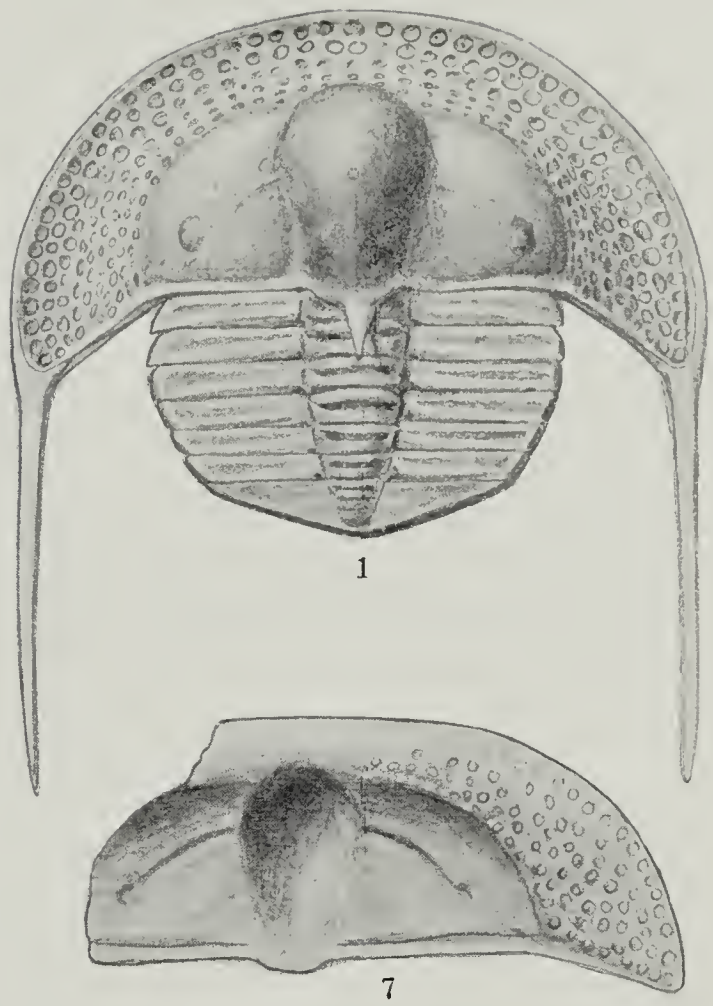
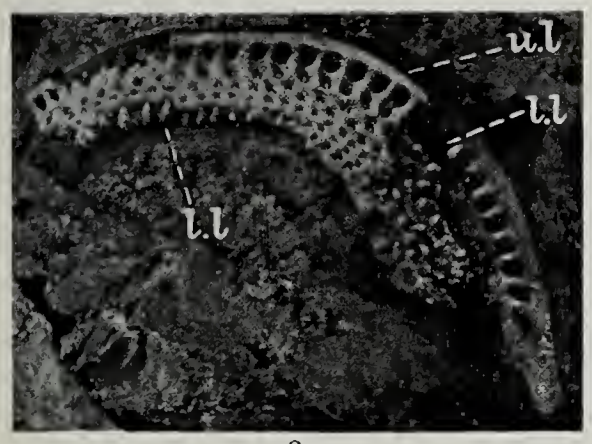
Plate 4.

Reedolithus carinatus (Ang.) Page 30.
All specimens from the Ampyx limestone.

Fig. 1. × 6. Restored specimen. (Drawn by the Author).
„ 2. ×23,7. Cephalon. Meraspid st. O (?) Gomnæs, Ringerike. No. H 514, Pal. Mus. Oslo. Kiær coll.
„ 3. ×23,7. The impression of the same specimen.
„ 4. ×23,7. Cephalon. Early Meraspid stage. Impression. Pits visible on the fringe. Gomnæs, Ringerike. No. H 422. Pal. Mus. Oslo. Aut. coll.
„ 5. ×23,7. Lower lamella of fringe in dorsal view. Meraspid stage. Girder visible. Genal spine broad. Gomnæs, Ringerike. No. H 531. Pal. Mus. Oslo. Kiær coll.
„ 6. ×23,7. Lateral view.
„ 7. ×23,7. Cephalon. Meraspid stage. Impression. Gomnæs, Ringerike. No. H 420 Pal. Mus. Oslo. Aut. coll.
„ 8. ×23,7. Fringe. Anterio-lateral portion. Young stage. The radial sulci indicate a development of pits. Gomnæs, Ringerike. No. H 429. Pal. Mus. Oslo. Kiær coll.
„ 9. × 6. Fringe. Dorsal view. Radial sulci visible on the upper lamella (u. l.). l.l. = lower lamella. Gomnæs, Ringerike. No. H 430. Pal. Mus. Oslo. Kiær coll.
„ 10. × 6. Neotype. Cephalon. (Spec. phot. covered with NH_4Cl). No. H 460. Gomnæs, Ringerike. Pal. Mus. Oslo. Kiær coll.
„ 11. × 6. Anterior view.
„ 12. × 6. Cephalon. Surface of shell smooth. Lateral eye tubercles (l. e.) very big. Huk, Bygdø, Oslo. No. H 512. Pal. Mus. Oslo, Brøgger coll.
„ 13. × 6. Lower lamella of fringe in dorsal view. Girder visible (g). gs = genal spine. Gomnæs, Ringerike. No. 458. Pal. Mus. Oslo. Kiær coll.







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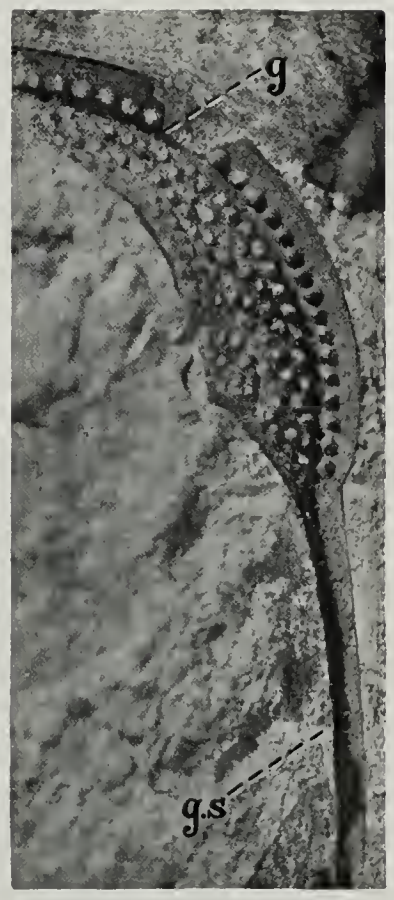

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Plate 5.

Reedolithus carinatus (Ang.). Page 30.
All specimens from the Ampyx limestone.

Fig. 1. × 9,7. Cephalon. Meraspid stage. Huk, Bygdø, Oslo. No. H. 518. Pal. Mus. Oslo. Brøgger coll.

„ 2. × 9,7. Cephalon. Anterior view. Huk, Bygdø, Oslo. No. H. 520. Pal. Mus. Oslo. Brøgger coll.

„ 3. × 6. Cephalon. Young stage. Well preserved specimen with lateral eye tubercles (l. e.). Huk, Bygdø, Oslo. No. H 516. Pal. Mus. Oslo. Brøgger coll.

„ 4. × 6. Cephalon. Young stage. Lateral view. Glabellar furrows appear as dark spots. Median eye tubercle (m. e) and occipital spine (oc. sp.) preserved. Huk, Bygdø, Oslo. No. H 517. Pal. Mus. Oslo. Brøgger coll.

„ 5. × 6. Cephalon. Young stage. Gomnæs, Ringerike. No. H 441. Pal. Mus. Oslo. Kiær coll.

„ 6. × 6. Anterior view.

„ 7. × 6. Lateral view.

„ 7. × 6. Enrolled young specimen. th. = thorax. g. = girder. Huk, Bygdø, Oslo. No. H 468. Pal. Mus. Oslo. Brøgger coll.

„ 9. × 6. Cephalon. Oc.s = occipital spine. Huk, Bygdø, Oslo. No. H 523. Pal. Mus. Oslo. Brøgger coll.

„ 10. × 9,7. Internal cast of lateral eye tubercle (l. e.). Gomnæs, Ringerike. No. H 452. Pal. Mus. Oslo. Kiær coll.

„ 11. × 6. Cephalon. Gomnæs, Ringerike. No. H 513. Pal. Mus. Oslo. Kiær coll.

„ 12. × 6. Nearly complete thorax and pygidium. Gomnæs, Ringerike. No. H 454. Pal. Mus. Oslo. Kiær coll.

„ 13. × 6. Cephalon. Anterio-dorsal view showing radial sulci and concentric lists on fringe. Gomnæs, Ringerike. No. H 451. Pal. Mus. Oslo. Kiær coll.

„ 14. × 6. Part of cephalon with occipital spine (oc. s.) Gullerud, Ringerike. No. H 466 Pal. Mus. Oslo. Brøgger coll.

„ 15. × 2. Fringe with genal spine. Gomnæs, Ringerike. No. 436. Pal. Mus. Oslo. Kiær coll.

„ 16. × 1,3. A number of specimens. a, b. enrolled. Gomnæs, Ringerike. a, b = No. H 431 and H 438. Pal. Mus. Oslo. Kiær coll.

„ 17. × 6. Cephalon Anterio-lateral view showing direction of occipital spine (oc. s.) Gullerud, Ringerike. No. H 535. Pal. Mus. Oslo. Brøgger coll.

„ 18. × 6. Lateral portion of fringe. Medio-ventral view showing lower lamella with girder (g) terrassic lines and integument atachment (i. a.). Gullerud, Ringerike. No. H. 465. Pal. Mus. Oslo. Brøgger coll.

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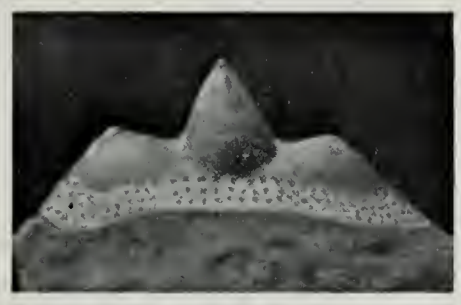

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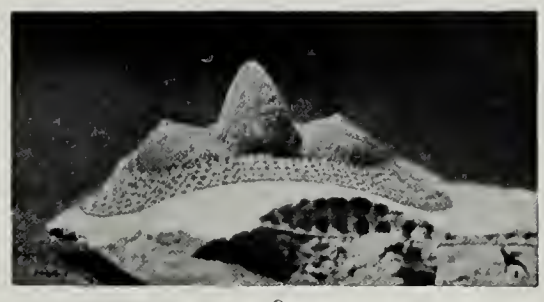

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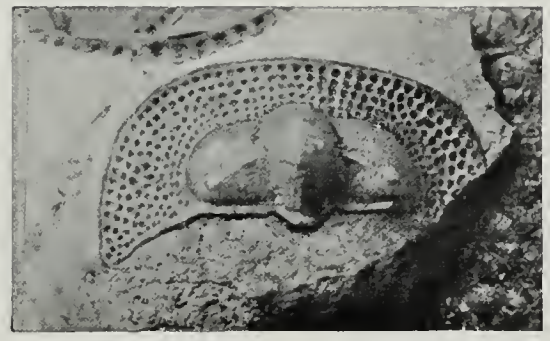

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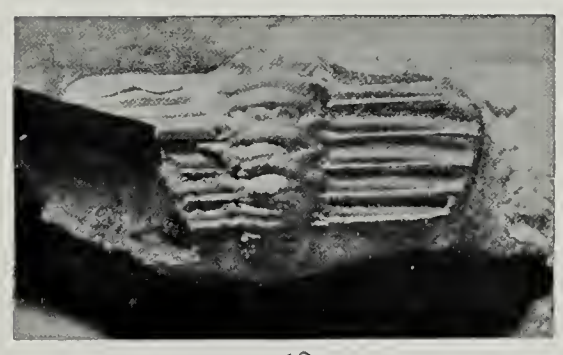

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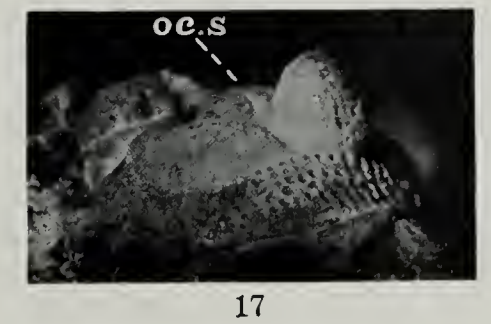

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18

Plate 6.

No retouche.

Cryptolithus dicors (Ang.) Page 40.

Fig. 1 a. × 5. Neotype Cephalon with lower lamella of fringe. Upper Chasmops limestone, Nakholmen, Oslo. No. Ar. 2298. Riksmus. Stockholm. G. Holm coll.

„ 1 b. × 5. Dorso-lateral view.

„ 1 c. × 5. Anterior view.

„ 2. × 4. Fringe. Ventral view showing lower lamella with faint girder (g) (Phot. NH_4Cl). Upper Chasmops limestone. Nakholmen, Oslo. No. H 367. Pal. Mus. Oslo.

„ 3. × 3,3. Pygidium. Upper Chasmops limestone. Nakholmen, Oslo. No. H 364. Pal. Mus. Oslo.

„ 4. × 9,7. Impression of upper lamella of fringe. Upper Chasmops limestone. Nakholmen, Oslo. No. Ar. 2298 Riksmus. Stockholm. G. Holm coll.

„ 5. × 9,7. Fringe. Ventral view. Meraspid stage II? Upper Chasmops limestone. Nakholmen, Oslo. No. H 586. Pal. Mus. Oslo.

„ 6. × 9,7. Pygidium, Meraspid stage. Upper Chasmops limestone. Nakholmen, Oslo. No. Ar. 2301. Riksmus. Stockholm. G. Holm coll.

„ 7. × 9,7. Fringe. Impression of upper lamella. Upper Chasmops limestone. Nakholmen, Oslo. No. Ar. 2299. Riksmus. Stockholm. G. Holm coll.

„ 8 a. × 2. Cephalon. A big specimen (phot. NH_4Cl). Upper Chasmops limestone. Nakholmen, Oslo. No. H 361. Pal. Mus. Oslo.

„ 8 b. × 2. Profile.

„ 9. × 16,7. Median eye tubercle (m. e.) of fig. 1 a.

„ 10. × 3,3. Pygidium with part of upper lamella of fringe. (Phot. NH_4Cl). Upper Chasmops limestone. Nakholmen, Oslo. No. H 363. Pal. Mus. Oslo.

„ 11. × 9,7. Lower lamella of fringe. Dorsal view showing girder and irregular pits on outer band. Upper Chasmops limestone, Nakholmen, Oslo. No. Ar. 2298. Riksmus. Stockholm. G. Holm coll.

„ 12. × 4. Outer band of ventral fringe. g = girder. g.s. = genal spine. Upper Chasmops limestone, Nakholmen, Oslo. No. Ar. 2303. Riksmus. Stockholm. G. Holm coll.

Cryptolithus conf. *portlocki* (Salter). Page 44.

„ 13. × 2. Cephalon without glabella (phot. NH_4Cl). Upper Chasmops zone. Husebergø, Oslo. No. H 301. Pal. Mus. Oslo.

Cryptolithus sp. Page 44.

„ 14. × 2. Cephalon with lower lamella of fringe (phot. NH_4Cl). Bryozoe layers. Fjicha, Dalarne, Sverige. (No. 20). Geol. Inst. Lund. Törnquist coll.

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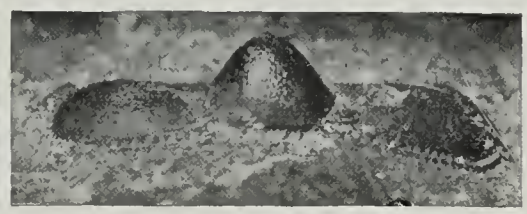
1b

1a

3

4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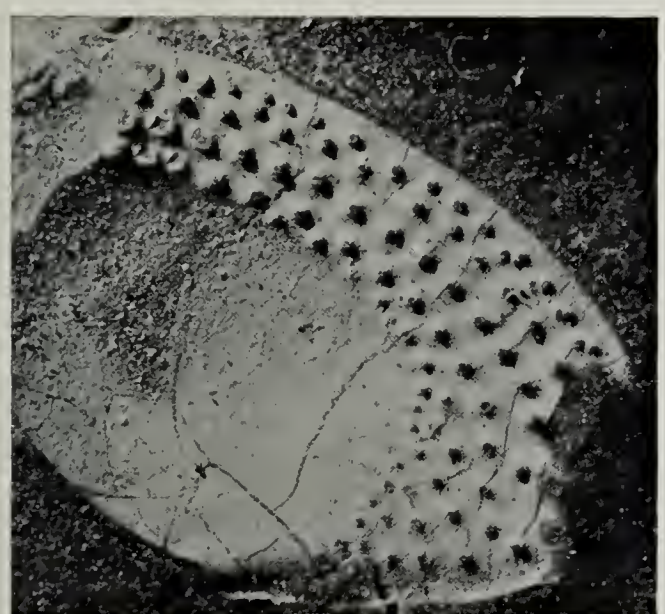
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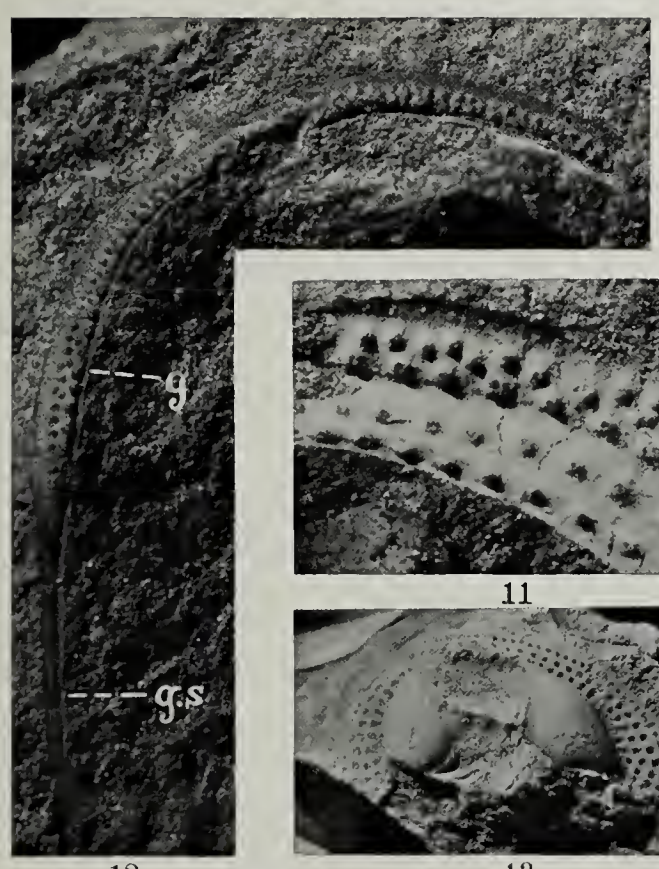
8b

8a



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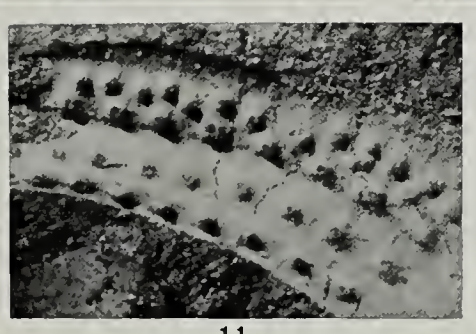
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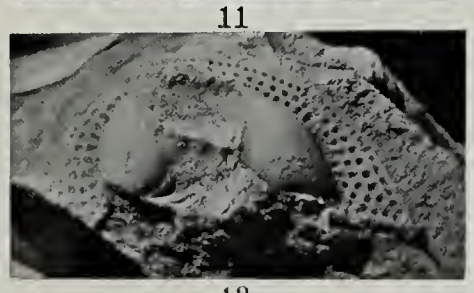
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Plate 7.

No retouche.

Tretaspis seticornis (His.). Page 55.

All specimens from the black Trinucleus shale of Sweden.

Fig. 1. ×23,7. Cephalon. Meraspid stage O. Genal spines preserved. Vikarbyn, Dalarne. (No. 10 a). Geol. Inst. Lund. Törnquist coll.

„ 2 a. ×23,7. Cephalon and pygidium. St. O. Vikarbyn, Dalarne (no. 12 a, b). Geol. Inst. Lund. Törnquist coll.

„ 2 b. ×16,7. The same.

„ 3 a. ×23,7. Cephalon. St. O. Median tubercle, alae and marginal suture visible. Motala, Østergøtland (no. 21 H). Geol. Inst. Lund. Törnquist coll.

„ 3 b. ×16,7. The same.

„ 4. ×23,7. Fringe, ventral view. St. O. "Pseudogirder". Vikarbyn, Dalarne (no. 12 d). Geol. Inst. Lund. Törnquist coll.

„ 5. ×23,7. Fringe, ventral view of anterior portion. St. I. Østergötland (no. 21 d). Geol. Inst. Lund. Törnquist coll.

„ 6. ×23,7. Lateral portion of fringe with genal spine, ventral view. St. I. Broad lower marginal rim. Vikarbyn, Dalarne. (No. 11 d). Geol. Inst. Lund. Törnquist coll.

„ 7. ×16,7. Cephalon. St. I. Dalarne no. Ar. 2294 Riksmus. Stockholm.

„ 8. ×16,7. Nearly complete specimen. St. I. Dalarne. No. Ar. 2287. Riksmus. Stockholm.

„ 9. ×16,7. Cephalon. St. II. Shell beautifully preserved. Median tubercle very distinct. Vikarbyn, Dalarne. (No. 12 e). Geol. Inst. Lund. Törnquist coll.

„ 10. ×16,7. Cephalon. St. II. Lateral eye tubercle distinct. Vikarbyn, Dalarne. (No. 12 g). Geol. Inst. Lund. Törnquist coll.

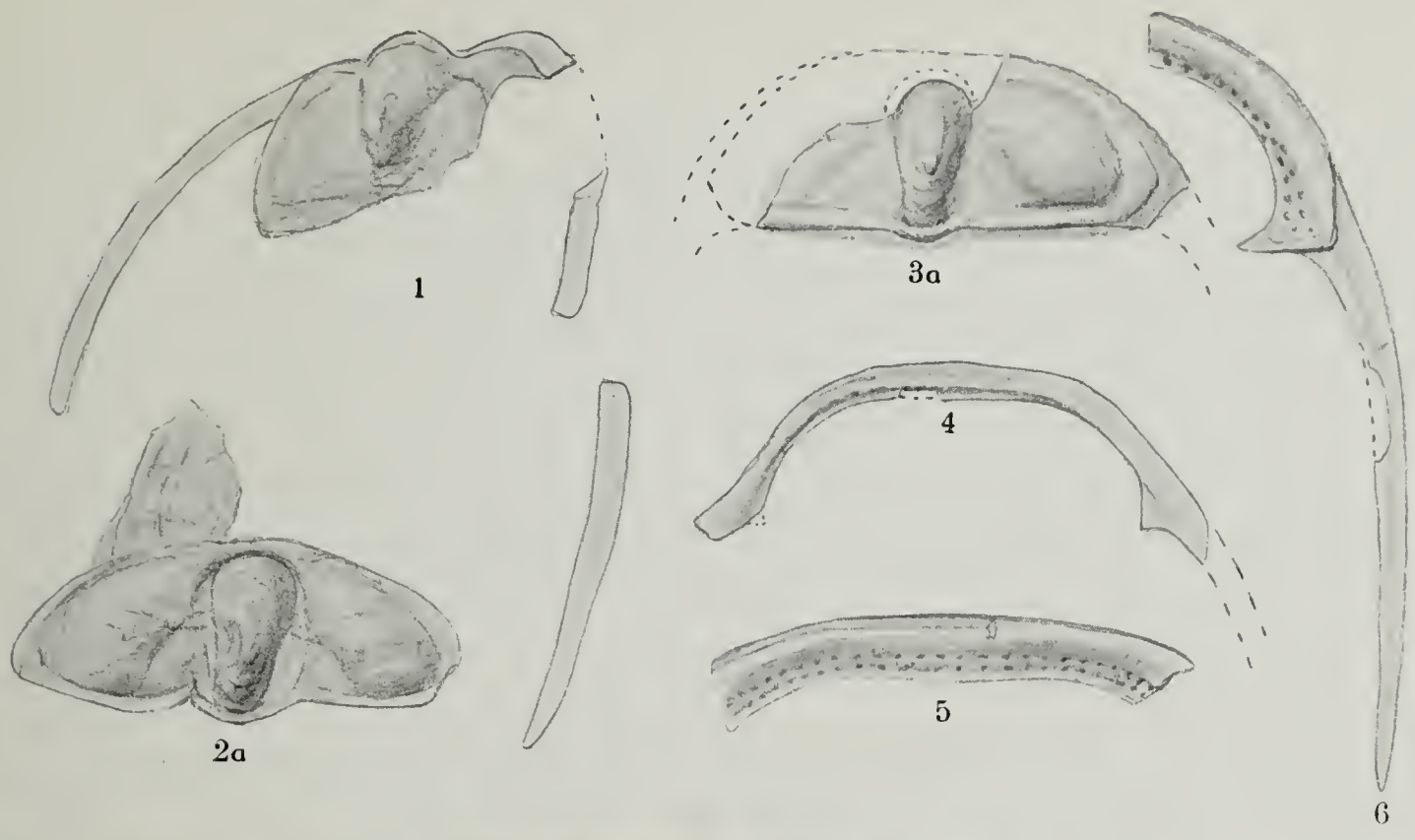
„ 11. ×16,7. Lower lamella of fringe. St. II. Dorsal view showing "pseudogirder" outside the faint girder (g). Vikarbyn, Dalarne. (No. 11 a). Geol. Inst. Lund. Törnquist coll.

„ 12. ×16,7. Enrolled specimen. St. II. Vikarbyn, Dalarne. (No. 11 c). Geol. Inst. Lund. Törnquist coll.

„ 13. × 9,7. Cephalon with impression of pygidium (p. g.). St. III. Vikarbyn, Dalarne. (No. 16). Geol. Inst. Lund. Törnquist coll.

„ 14. × 4. Lower lamella of fringe. St. IV—V. Dorsal view showing distinct girder. (g). Østergötland. (No. 21,o). Geol. Inst. Lund. Törnquist coll.

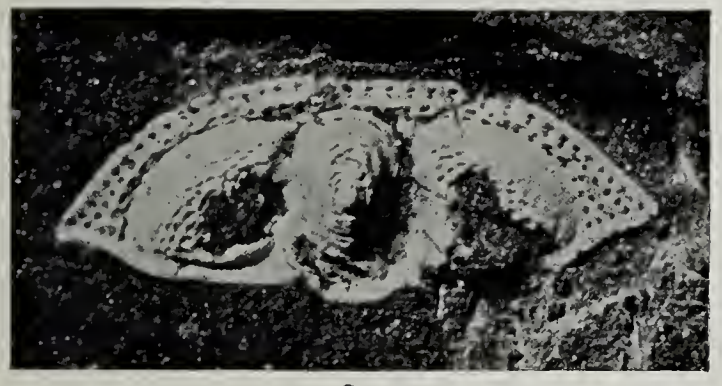
„ 15. × 4. Cephalon. St. IV—V. Østergøtland. (No. 21 e). Geol. Inst. Lund. Törnquist coll.



3b

2b

7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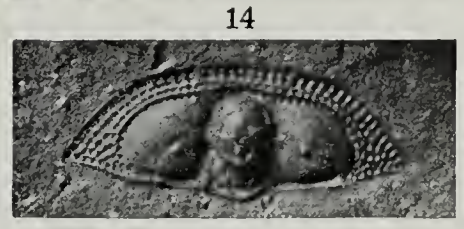
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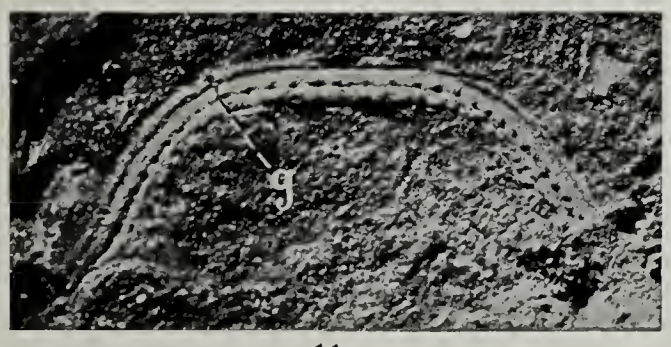

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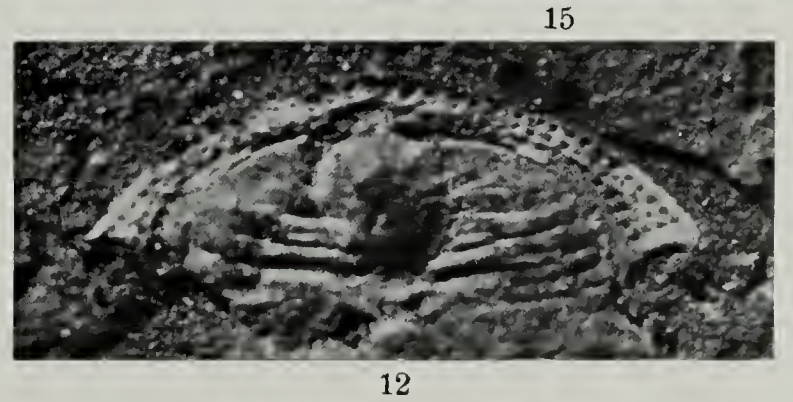
12

Plate 8.

No retouche.

Tretaspis seticornis (His.). Page 55.

All specimens from the black Trinucleus shale of Sweden.

Fig. 1. ×12,1. Complete specimen St. III. Lower lamella of fringe not present. Three thoracic segments (3 th), Vikarbyn, Dalarne. No. Ar. 2286. Riksmus. Stockholm.

„ 2. ×12,1. Complete specimen St. IV. Impression. Lower lamella of fringe not present. Four thoracic segments (4 th), Vikarbyn, Dalarne. (No. 8). Geol. Inst. Lund. Törnquist coll.

„ 3. ×12,1. Complete specimen. St. V. Lower lamella of fringe not present. Five thoracic segments (5 th). Vikarbyn, Dalarne. (No. 1). Geol. Inst. Lund. Törnquist coll.

„ 4. × 6,5. Complete specimen. Holaspid stage. Lower lamella of fringe not present. Six thoracic segments (6 th). Draggån, Dalarne. No. Ar. 2296. Riksmus. Stockholm.

„ 5. × 1,7. Complete specimen. Adult. Dalarne no. Ar. 2290. Riksmus. Stockholm. B. Nilsson coll.

„ 6. × 2.5. Fragments of fringe. Lower lamella with girder (g). Vikarbyn, Dalarne. (No. 15). Geol. Inst. Lund. Törnquist coll.

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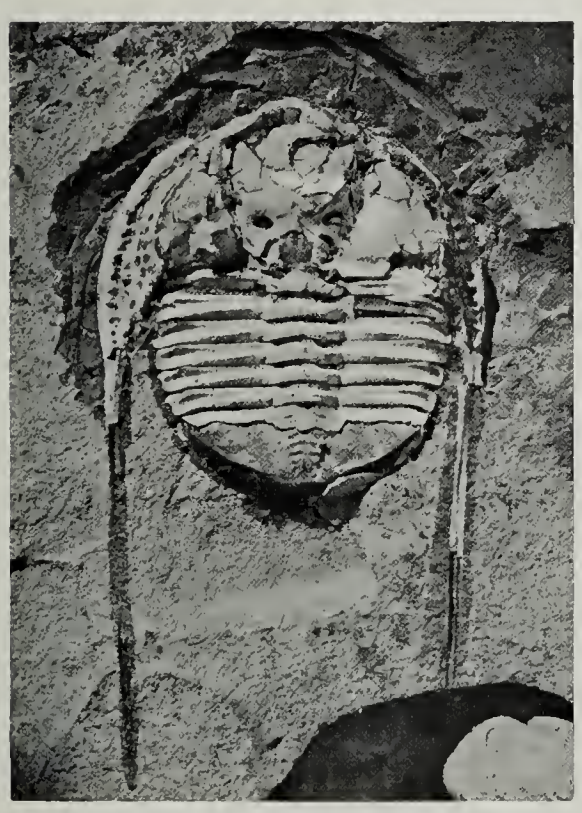

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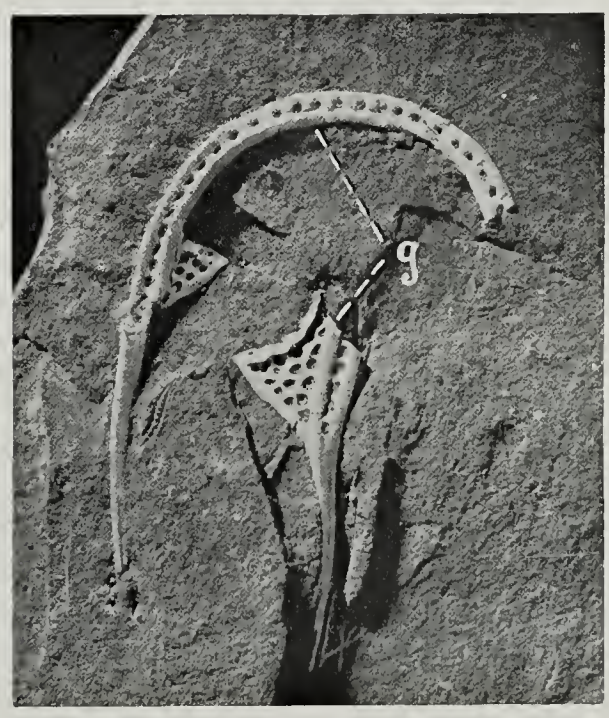

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Plate 9.

Tretaspis cerioides (Ang.). Page 45.

All specimens from upper Chasmops limestone, Norway.

Fig. 1 a. × 3,6. Neotype. Cephalon with both lamella of fringe. (Phot. NH_4Cl). Norderhov. Ringerike. No. H 381. Pal. Mus. Oslo. Aut. coll.

„ 1 b. × 3,6. Lateral view.

„ 1 c. × 3,6. Anterior view.

„ 1 d. × 9,7. Anterio-ventral view showing glabella (gl.), marginal suture (mg. s.) and outer band with girder (g.).

„ 2 a. × 6. Cephalon. Young stage. (Phot. NH_4Cl). Norderhov, Ringerike. No. H 370. Pal. Mus. Oslo. Aut. coll.

„ 2 b. × 6. Anterior view.

„ 3. × 6. Cephalon. Anterio-lateral view. The strongly reticulated surface of shell, beautifully preserved. The reticulating (r. l.) and concentric lists (cn. l.) visible. Ringsåsen, Ringerike. No. 2317. Riksmus. Stockholm. G. Holm coll.

„ 4. × 3,6. Pygidium. Ringsåsen, Ringerike. No. H. 743. Pal. Mus. Oslo. Holtedahl coll.

Tretaspis cerioides (Ang.) var. *angelini* n. var. Page 48.

„ 5 a. × 3,6. Holotype. Cephalon. Terneholmen, Asker. No. H 526. Pal. Mus. Oslo. Kiær coll.

„ 5 b. × 3,6. Anterior view.

„ 5 c. × 3,6. Lateral view.

„ 6 a. × 9,7. Cephalon. Meraspid stage. Terneholmen, Asker. No. H 232. Pal. Mus. Oslo. Kiær coll.

„ 6 b. × 9,7. Anterior view.

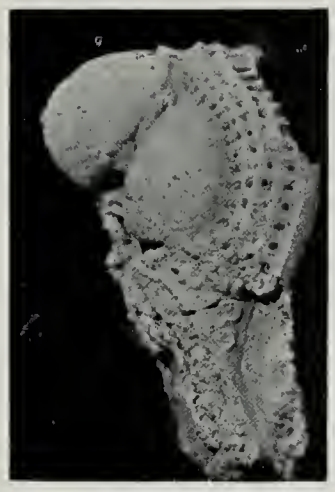
„ 7. × 6. Lower lamella of fringe. Posterio-ventral view showing the strong girder (g.) with terrace lines, and the hollow pillars (h. p.). Terneholmen, Asker. Kiær coll.

„ 8. × 9,7. Cephalon. Anterio-lateral view of upper lamella of fringe. Meraspid stage I (?). Terneholmen, Asker. No. H 240. Pal. Mus. Oslo. Kiær coll.

„ 9. × 3,6. Pygidium. Terneholmen, Asker. No. H 243. Pal. Mus. Oslo. Kiær coll.

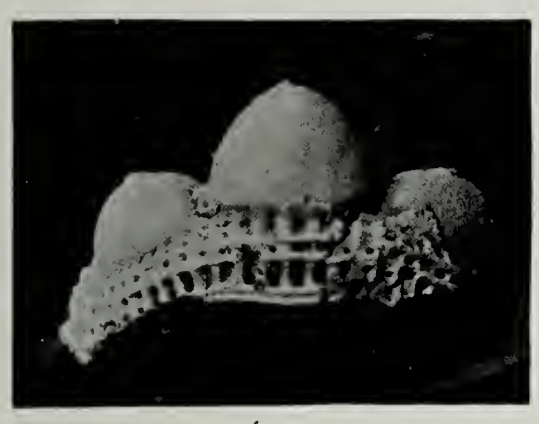
„ 10. × 6. Cephalon. Lateral view of well preserved specimen showing marginal suture (mg. s.) and glabellar furrows. Terneholmen, Asker. No. H 593. Pal. Mus. Oslo. Kiær coll.

1a



1b

1d



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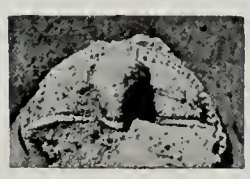
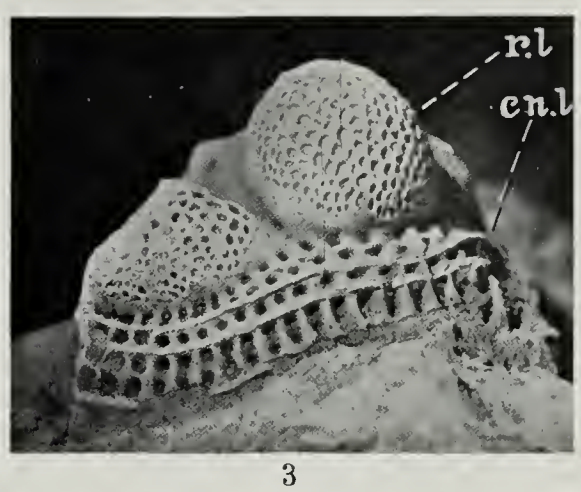


2a

2b



3

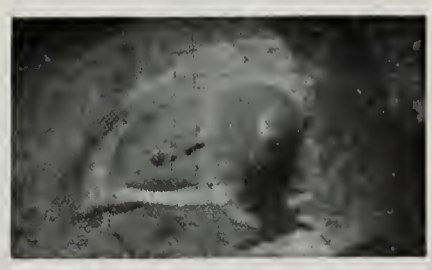
5b

4

6b

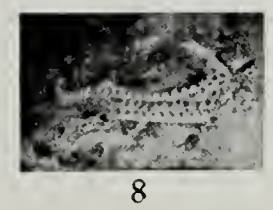
5a

5c



6a

7



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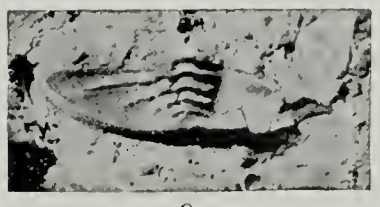

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Plate 10.

Tretaspis kiæri n. sp. Page 50.
All specimens from lower Trinucleus limestone Frognø, Ringerike.
Pal. Mus. Oslo. KIÆR coll.

Fig. 1 a. × 2,3. Holotype. Cephalon. Internal cast. No. H 197.
„ 1 b. × 2,3. Anterior view.
„ 1 c. × 2,3. Lateral view.
„ 2. × 2,3. Pygidium. Internal cast. No. H 223.
„ 3 a. × 6,5. Cephalon. Lateral view showing internal cast of upper lamella of fringe (u. l.) and the inner surface of the lower lamella (l. l.) with girder. l. n. = lateral eye tubercle. No. H 338.
„ 3 b. × 11. Details of fig. 3 a. Internal cast of upper lamella with the shell preserved in the bottom of the pits. The black spot indicates the opening of the hollow pillar.
„ 4. × 6,5. Pygidium. Internal cast, with muscular impressions, appendifers (ap.). No. H 622.
„ 5. × 6,5. Anterior portion of lower lamella of fringe. Dorsal view. Pits in radial sulci on inner band. g = girder. No. H 341.
„ 6. × 6,5. Portion of fringe. Dorso-lateral view. The internal cast of upper lamella (u. l.) shows the radial sulci on the brim. The correspondance in the arrangement of pits may be studied. Lower lamella (l. l.) shows rather irregular arrangement of pits laterally.

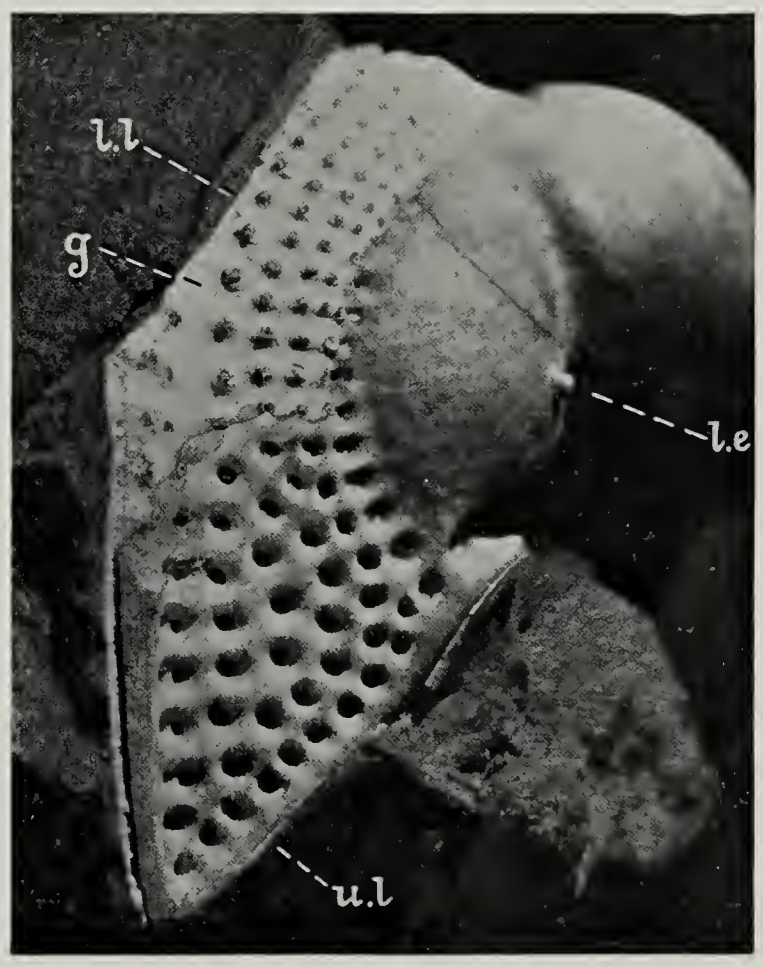
1a

1b

2

1c

3b



3a

4

5

6

Plate 11.

Fig. 3—7, and 12, are not retouched.

Tretaspis seticornis (His.). Page 55.

Fig. 1 a. × 2. Cephalon with two thoracic segments. (Phot. NH_4Cl). Trinucleus shale, Frogno, Ringerike. No. H 325. Pal. Mus. Oslo. Kiær coll.

„ 1 b. × 2. Lateral view.

„ 1 c. × 2. Anterior view.

„ 2. × 6. Part of cephalon with fringe. Anterio-dorsal view. Shell only preserved in the lower lamella of fringe (l. l.). g. = girder, u. l. = upper lamella, gl. = glabella, an. p. = antennuary pit. Upper Trinucleus limestone, Frognø, Ringerike. No. H 128. Pal. Mus. Oslo. Kiær coll.

„ 3. × 6. Internal cast of glabella with median eye tubercle (m. e.) and lists running anterio-laterally. Trinucleus shale, Frogno, Ringerike. No. H 75. Pal. Mus. Oslo. Kiær coll.

„ 4 a. ×20. Portion of marginal rim. Lateral view. Small pits suggesting canal opening (co) visible. Trinucleus shale Amtjärn, Dalarne. No. Ar. 2293. Riksmus. Stockholm. B. Nilsson coll.

„ 4 b. ×20. More ventral view showing the broken marginal suture (mg. s).

„ 4 c. ×20. Ventral view. Canal openings visible between the terrace lines (ta.). h. p. = hollow pillars, pits of fringe-

„ 5. ×20. Median eye tubercle (m. e.). 5 small pits visible on the tubercle (compare fig. 37 c p. 87). Surface of the shell of glabella faintly reticulated. Trinucleus shale Frogno, Ringerike no. H 103. Pal. Mus. Oslo. Kiær coll.

„ 6. ×20. Median eye tubercle (m. e.). Postorio-lateral view. (Compare fig. 37 d, p. 87). Shell surface of glabella smooth. Trinucleus shale, Frognø, Ringerike. No. H 100. Pal. Mus. Oslo. Kiær coll.

„ 7. ×20. Lateral eye tubercle (l. e.) of the same specimen. Surface of tubercle quite smooth.

Tretaspis latilimbus (Linrs). Page 67.

„ 8. × 6. Anterior fringe. Anterio-dorsal view showing pits on upper (u. l.) and lower (l. l.) lamella. An. p. = Antennuary pits. Trinucleus limestone, Lindø, Oslo. No. H 276. Pal. Mus. Oslo.

„ 9. × 3,6. Impression of pygidium with segments of thorax. Appendifers (ap.) visible on rachis. Articulating joint (a. j.) of the thoracic segments well preserved. Upper Chasmops zone, Lindø, Oslo. No. H 297. Pal. Mus. Oslo.

„ 10. × 3,6. Portion of lower lamella of fringe. Ventral view. Hollow pillars, pits (h. p.) well preserved, showing a small opening in the bottom. Trinucleus limestone, Lindø, Oslo. No. H 601. Pal. Mus. Oslo.

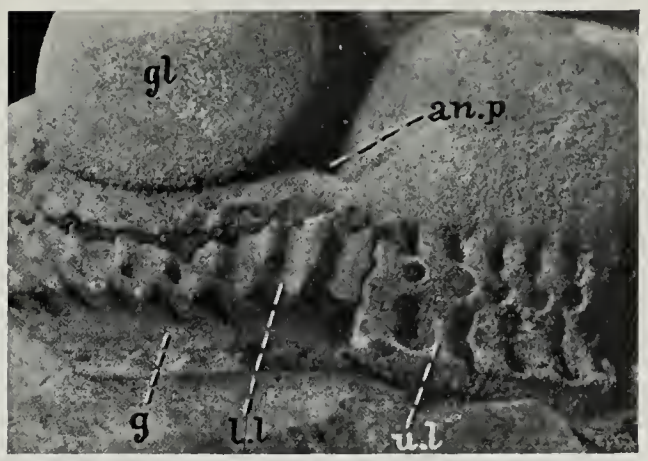
„ 11. × 3,7. Pygidium. Trinucleus limestone, Lindø, Oslo. No. H 270. Pal. Mus. Oslo.

Tretaspis kiæri n. sp. Page 100.

„ 12. ×20. Marginal rim. Lateral view showing canal opening (c. o.) and marginal suture (mg. s.). Lower Trinucleus limestone, Frognø, Ringerike. No. H 208. Pal. Mus. Oslo. Kiær coll.

1a

1b



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1c

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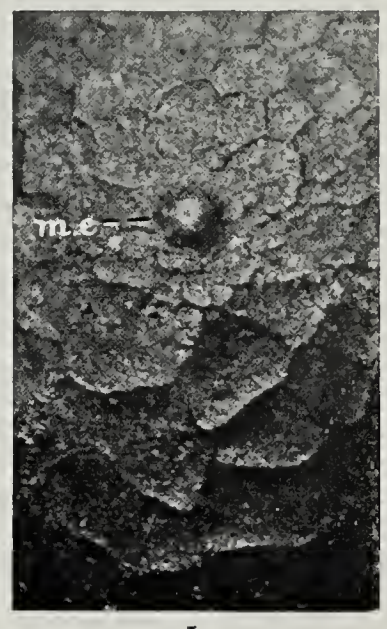

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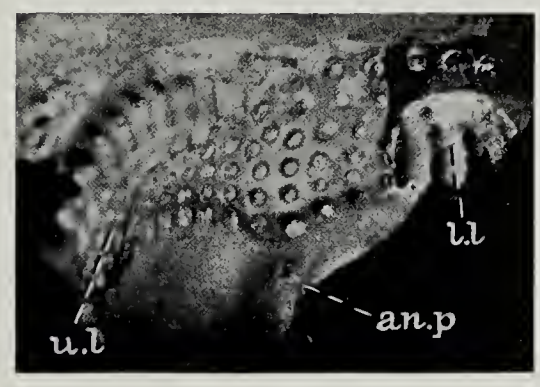
4a



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4b

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4c

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Plate 12.

No retouche.

Tretaspis seticornis (His.). Page 96.

All sections from the upper Trinucleus limestone Frognø, Ringerike.

Pal. Mus. Oslo. Kiær coll.

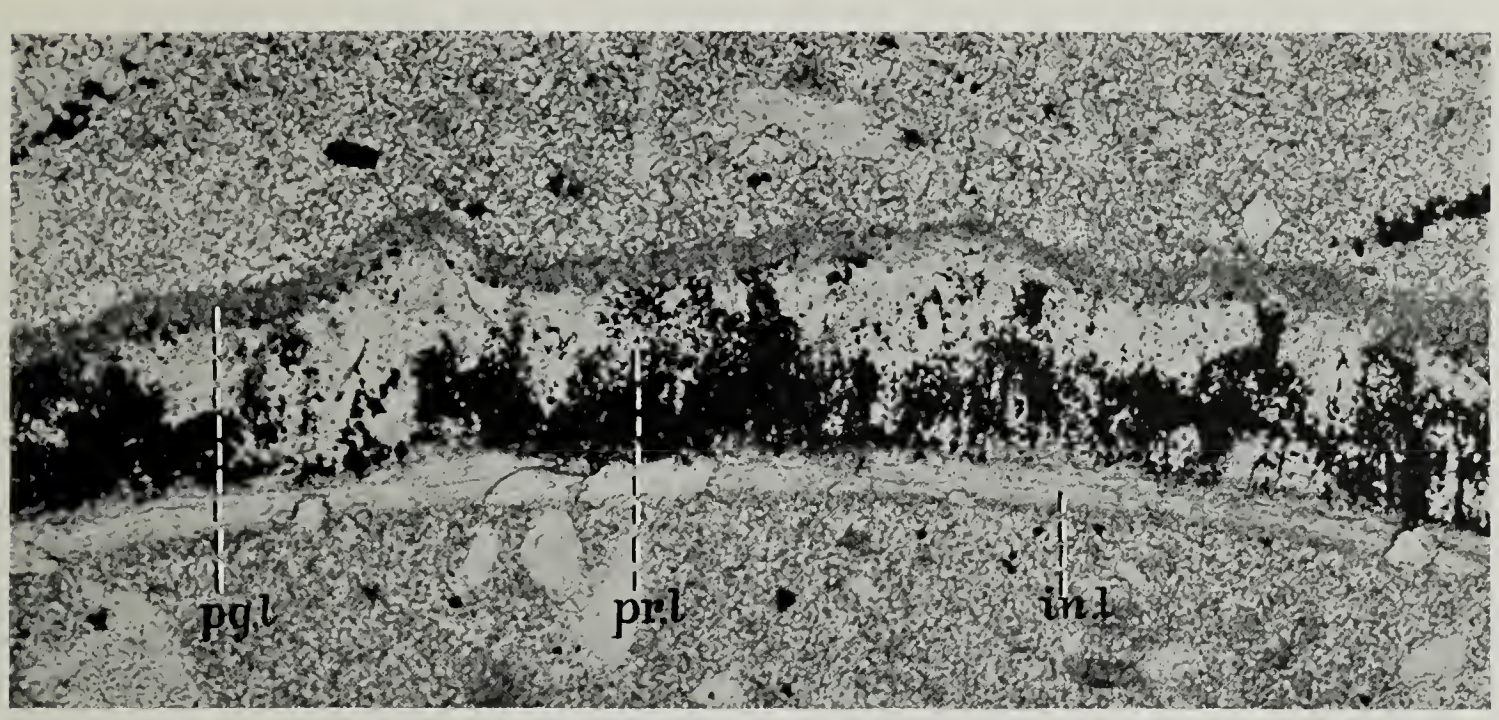
Fig. 1. × 150. Glabella. Cross section of the shell. Three layers may be recognised: The pigment layer (pg. l.), the principle layer (pr. l) and the inner layer (in. l.). Radial arrangement of the pyrrite grains visible. No. T, II. 9.

„ 2, × 100. Occipital furrow. Cross section of shell. Distinct radial arrangement of the pyrrite grains, indicating numerous tubercle or canaliculae (cl.) No. T. I. 29.

„ 3. × 75. Lateral eye tubercle. Cross section. A darker lenticular body (l.) indicated in the shell above the lateral eye (l. e.). Tubulae distinct. No. T. I. 29.

„ 4. × 100. Dorsal furrow. Cross section of shell. Possible traces of an outer layer of shell (o. l. ?). in. l. = inner layer. Very fine radial canaliculae (cl). Laminated structure of the principle layer indicated (la.). No. T. III. 21.

„ 5. × 100. Glabella near 2nd pair of glabellar furrows. Cross section of shell. The laminated structure of shell very distinct. Between the more distinct laminae (la.) several less marked may be traced. No. T. III. 20.



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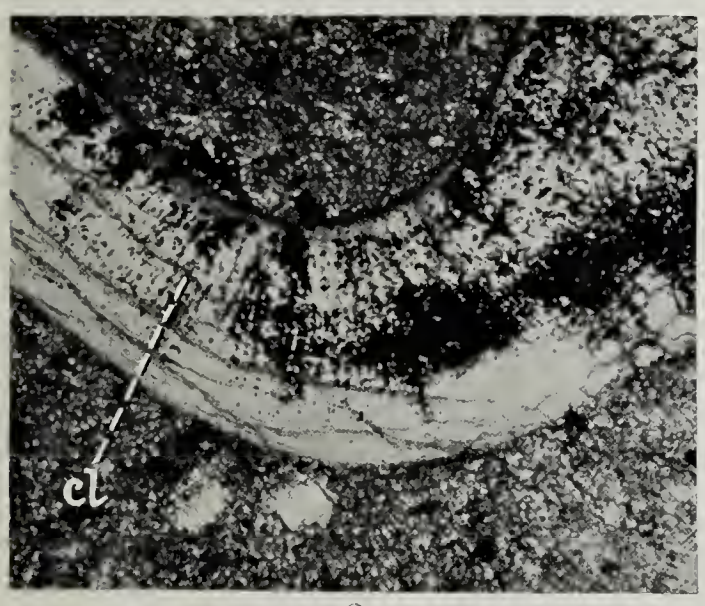

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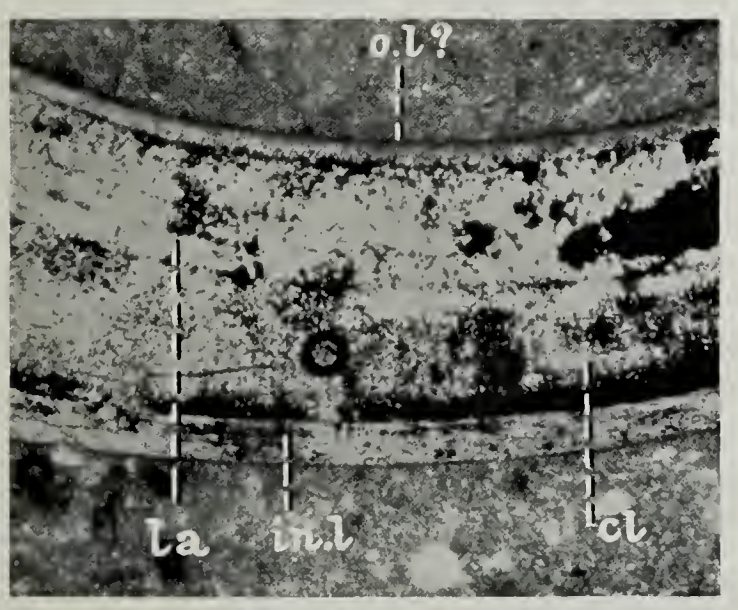

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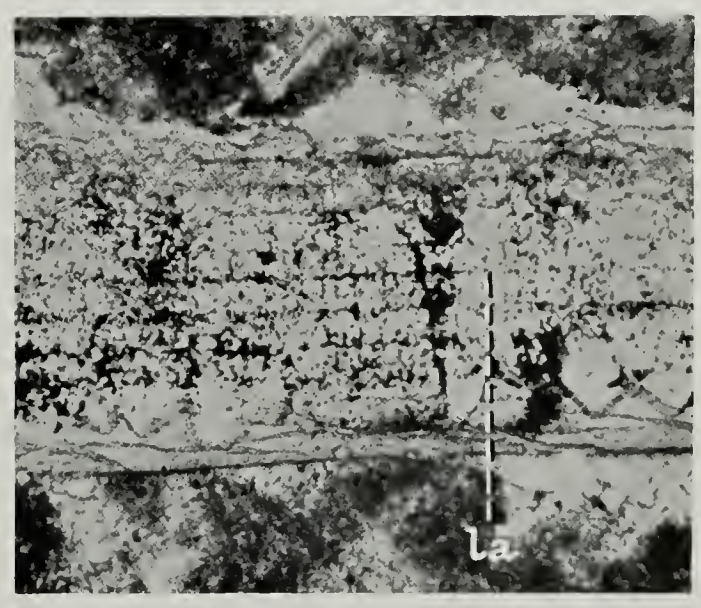

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Plate 13.

No retouche.

Tretaspis seticornis (His.). Page 89.

Fig. 1. × 38. Lateral eye tubercle (l. e.). Cross section. A darker lenticular body indicated in the shell above the eye (l.). Upper Trinucleus limestone, Frognø, Ringerike. No. T. III. 4. Pal. Mus. Oslo. Kiær coll.

„ 2. ×100. Lateral eye tubercle (l. e.). Cross section of a younger specimen. A distinct dark lenticular body visible in the shell above the tubercle (l.). Upper. Trinucleus limestone, Frognø, Ringerike. No. T. III. 24. Pal. Mus. Oslo Kiær coll.

Tretaspis kiari n. sp. Page 84.

„ 3. × 38. Median eye tubercle (m. e.). Cross section. Surface of glabella strongly reticulated. r. l. = reticulating list, cross section. The pigment layer of the shell indicated. Lower Trinucleus limestone, Frognø, Ringerike. No. T. I. 17. Pal. Mus. Oslo. Kiær coll.

Trinucleus bucculentus, Ang. Page 84.

„ 4. × 38. Median eye tubercle (m. e.). Longitudinal section. Shell of glabella with reticulating lists (r. l.) and radial stay lines (s. l.). Ogygia shale, Engervik, Asker. No. T. I. 25. Pal. Mus. Oslo. Kiær coll.

Tretaspis seticornis, (His.). Page 84.

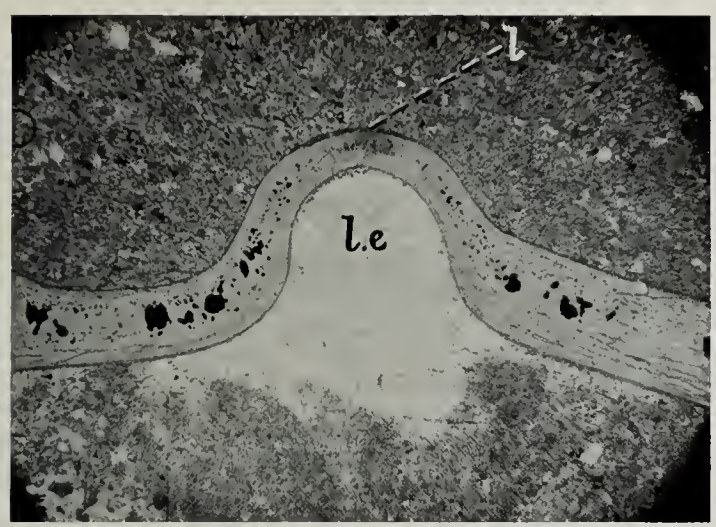
„ 5. × 75. Median eye tubercle (m. e.). Cross section of shell of young specimen. Upper Trinucleus limestone, Frognø, Ringerike. No. T. III. 27. Pal. Mus. Oslo. Kiær coll.

„ 6. × 75. Median eye tubercle (m. e.). Cross section of shell. A pyrrite-filled canal in the shell above the tubercle indicated. Upper Trinucleus limestone, Frognø, Ringerike. No. T. II. 9. Pal. Mus. Oslo. Kiær coll.

„ 7. × 75. Glabella. Cross section of shell showing reticulating lists (r. l.) and stay lines (s. l.) below. Pigment layer of shell well marked. Upper Trinucleus limestone. Ringsåsen, Ringerike, no. T. II. 17. Pal. Mus. Oslo. Brøggger coll.

Trinucleus bronni (Sars et Boeck). Page 100.

„ 8, × 38. Fringe. Cross section of lateral part Hollow pillars (h. p.) distinct. The marginal suture appear as a dark line crossing the shell (mg. s.). Shell pierced by numerous pyrrite-filled canals (c). Ogygia shale, Gomnæs, Ringerike. No. T. II. 10. Pal. Mus. Oslo. Aut. coll.



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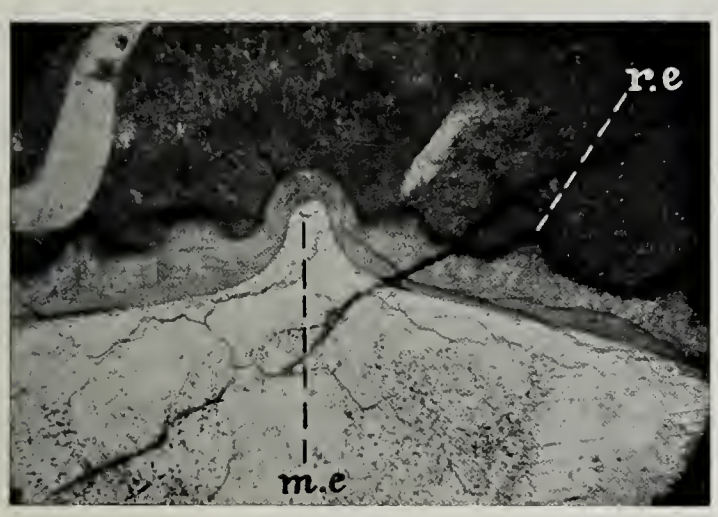

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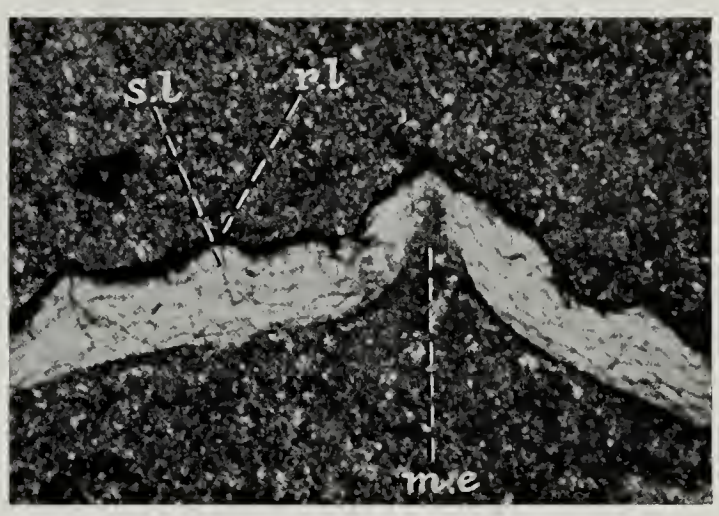

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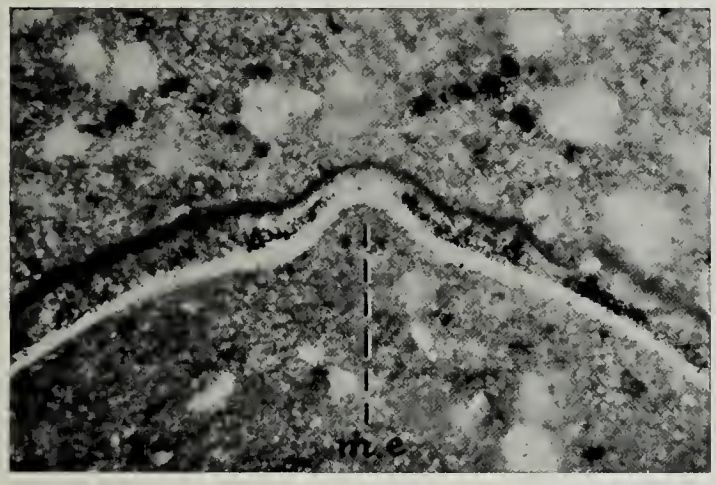

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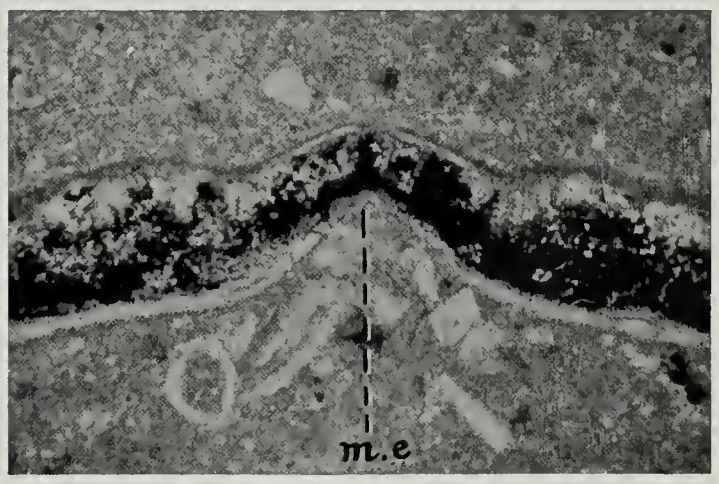

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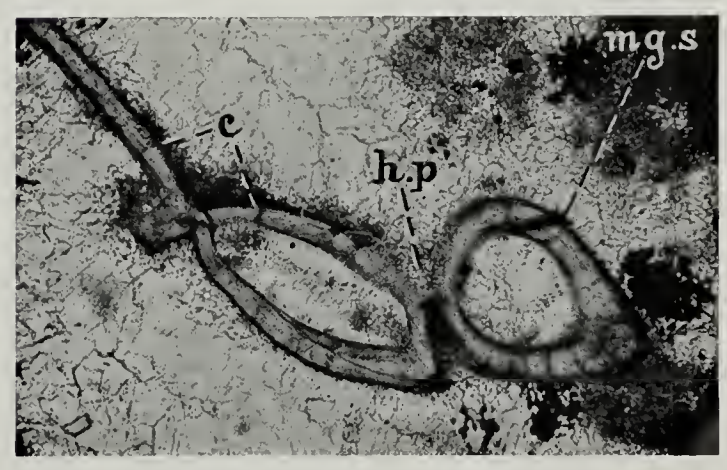

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Plate 14.

No retouche.

Tretaspis kiæri n. sp. Page 50.

Fig. 1. × 10. Cephalon. Median section. The steep fringe with the two lamellae visible. Girder (g) strong with well marked internal stay lines. c. l. = concentric lists. i. a. = integument attachment. mg. s. = marginal suture. oc. r. = occipital ring. r. l. = reticulating lists. Lower Trinucleus limestone, Frognø, Ringerike. No. T. I. 17. Pal. Mus. Oslo. Kiær coll.

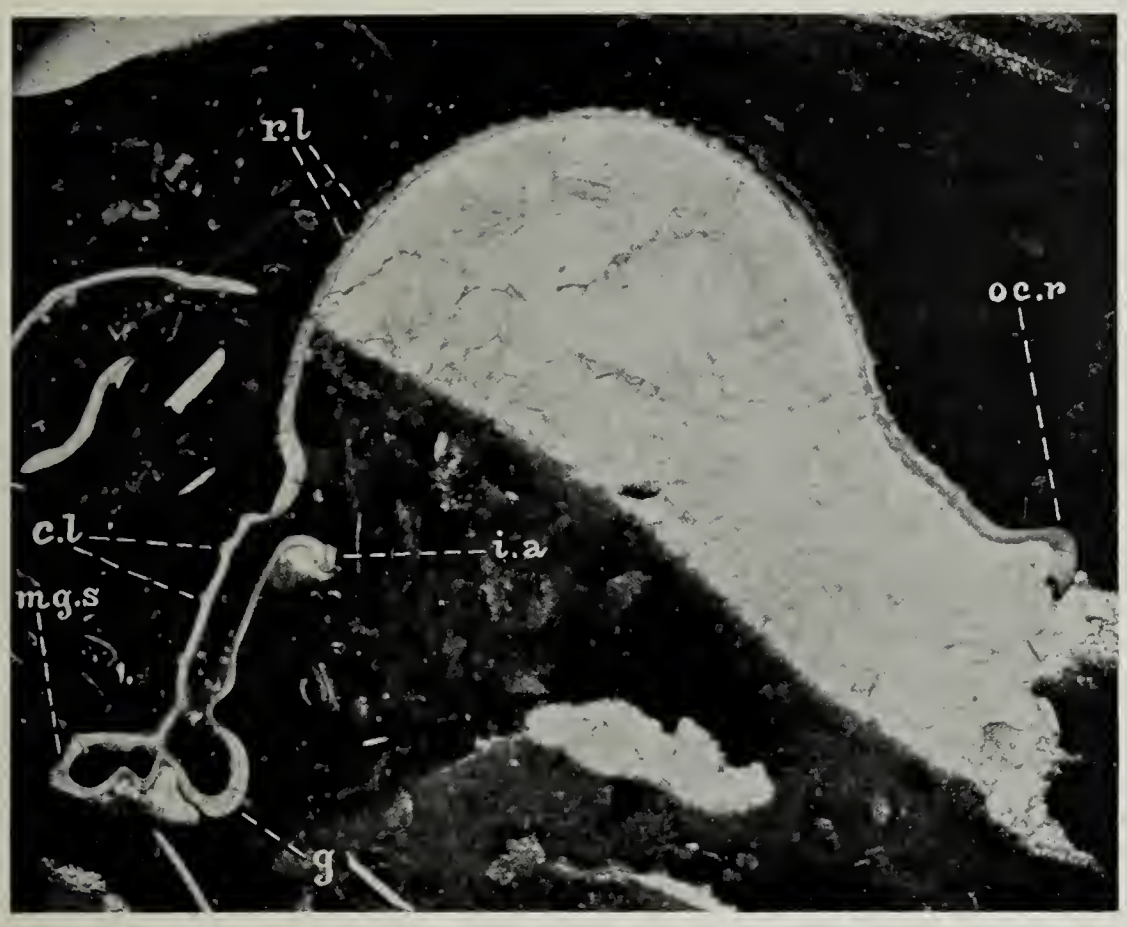
„ 2. × 10. Fringe. Median section. The hollow pillars (h. p.) very distinct. The suture visible across the shell in the hollow pillars. g = girder. Lower Trinucleus limestone, Frogno, Ringerike. No. T. II. 4. Pal. Mus. Oslo. Kiær coll.

„ 3. × 10. Fringe. Cross section of lateral portion. The open hollow pillars (h. p.) with the suture across the shell very distinct. mg. s. = marginal suture. g. = girder. Lower Trinucleus limestone, Frognø, Ringerike. No. T. I. 13. Pal. Mus. Oslo. Kiær coll.

Tretaspis seticornis (His.). Page 55.

„ 4. × 16. Fringe. Nearly median section showing the two lamellae with hollow pillars (h. p.) and girder (g.). Stay lines visible in the shell. They appear as terrace lines on the outer surface. Upper Trinucleus limestone, Frognø, Ringerike. No. T. II. 16. Pal. Mus. Oslo. Kiær coll.

„ 5. × 16. Thorax of enrolled specimen. Longitudinal section of rachis crossing the appendifers (ap.). The number of the segments is given ($th_3 - th_6$). Upper Trinucleus limestone, Frognø, Ringerike. No. T. III. 3. Pal. Mus. Oslo. Kiær coll.



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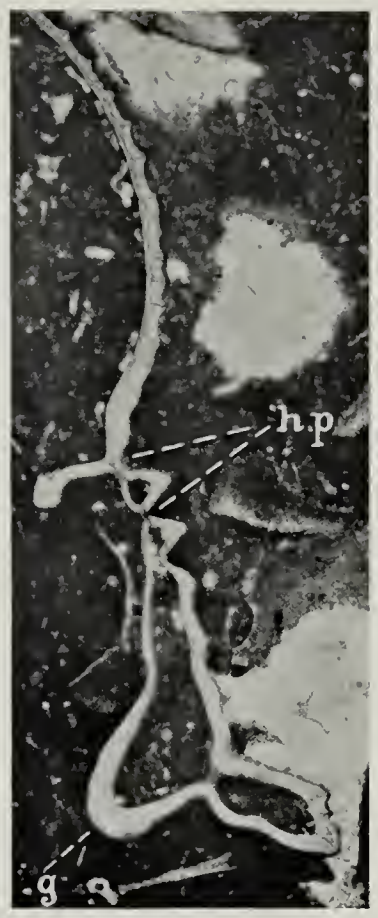

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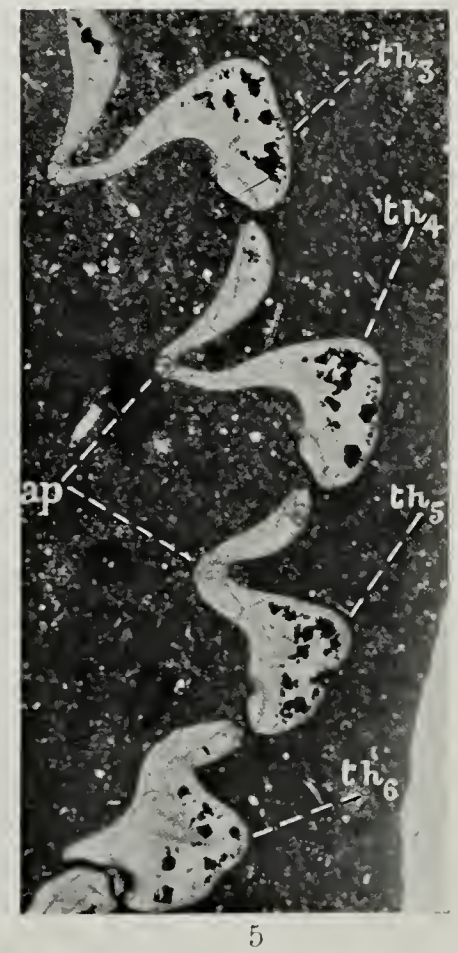

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